SPECIES ASSEMBLAGE STRUCTURE AND ECOMORPHOLOGICAL CONVERGENCE IN PERCIFORM FISHES (CICHLIDAE AND CENTRARCHIDAE) IN TROPICAL AND TEMPERATE FLOODPLAIN RIVERS

A Dissertation

by

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ABSTRACT

In this study, I used two independent perciform lineages (Neotropical Cichlidae and Nearctic Centrarchidae) to examine patterns of species richness and species coexistence at two spatial scales (e.g., macrohabitat and mesohabitat) and to examine inter-faunal patterns of ecomorphological convergence. The study was conducted during the low-water periods in four lowland rivers: the Cinaruco in Venezuela, the Tambopata in Peru, and the Neches and the Brazos rivers in Texas (USA). These rivers were chosen because of their similar characteristics, in terms of geomorphology, sediments, and water quality. The Cinaruco River and the Neches River have clear slightly-stained waters, whereas the Tambopata and the Brazos River have turbid waters with high loads of suspended sediments. I used morphological approaches as a surrogate to investigate patterns of species distribution in niche space, and predict patterns of species richness at different spatial scales. Despite high variation in the number of species in these two perciform assemblages, morphological analysis based on the means and standard deviations of nearest neighbor distance (NND) and mean distance to centroid (CD) revealed similar trends of morphological similarity in relation to species richness. Comparison of observed versus randomized data mesohabitat scale for all four rivers generally supported the niche expansion model of response to increase in species richness. At the scale of mesohabitats within rivers, most species assemblages appear to be organized by competitive interactions in accordance with the niche expansion model. The tropical species-rich Cinaruco River revealed particularly strong support for the

niche expansion model. Intercontinental comparison of functional morphology and diets based on analysis of stomach contents and stable isotope ratios indicated broad morphological and dietary overlap between cichlid and centrarchid assemblages. For the most part, morphological ordinations showed that the two groups have diversified in a parallel manner within the confines of ram-suction modes of prey ingestion. This study concludes that even though differences are observed in historical and stochastic factors structuring fish assemblages in different geographic regions, consistent patterns of convergence at the species and assemblage levels results from natural selection under similar environmental conditions.

DEDICATION

To my family

To Donald Charles Taphorn

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CHAPTER I

INTRODUCTION: MORPHOLOGICAL AND ECOLOGICAL CONVERGENCE IN NEOTROPICAL CICHLIDS AND NEARCTIC CENTRARCHIDS

Many Neotropical cichlids (Cichlidae) have evolved morphological and ecological traits that appear parallel to those of Nearctic centrarchids (Centrarchidae). These fishes, therefore, offer a unique opportunity to study patterns of morphological and ecological convergence. At first glance, cichlids and centrarchids seem to be closely related because both radiations have multicolored fishes, show similarities in reproductive behaviors such as nest construction and parental care (Perrone and Zaret 1979, Cook and Phillip 2009), occupy similar ecological niches, have comparable morphologies, and have similar feeding mechanics (e.g., pressure profiles in the buccal and opercular cavities during feeding (Norton and Brained 1993). This evolutionary convergence seems to have been driven by selection for similar trophic niches within similar habitat types.

The families Cichlidae and Centrarchidae belong to the order Perciformes. The family Cichlidae is contained within the sub-order Labroidei along with the families Pomacentridae (e.g., damselfishes, clownfishes), Embioticidae (e.g., surfperches), Odacidae (e.g., butterfishes), Labridae (e.g., wrasses), and Scaridae (e.g., parrotfishes). This classification is based, in part, on shared structures of the pharyngeal jaw apparatus (Kaufman and Liem 1982, Staissny and Jensen 1997). Cichlids represent one of the

most species-rich fish families (10% of extant teleost diversity) and are distributed across the principal fragments of the former Gondwana supercontinent, including Central and South America, Africa, Madagascar, the Middle East, and Southern India (Barlow 2000). The fossil record of the family Cichlidae indicates that it originated during the early Cretaceous period (~135 mya; Stiassny 1991, Farias et al. 1999). The great diversification of Neotropical cichlids appears to go back to the Late Cretaceous (> 90 mya, Chakrabarty 2006, Lundberg et al. 2010), a geological era when most of the earth experienced warm conditions and when many freshwater teleosts diversified, probably in response to new ecological opportunities (Losos and Mahler 2010). This burst of evolutionary diversification in cichlids seem to be associated with innovations in jaw structures (Liem 1973) and phenotypic adaptations linked to feeding and reproduction such as mouth-brooding (López-Fernández et al. 2005). In the Neotropics, the family is comprised of 60 genera and at least 600 species (Lopez-Fernandez et al. 2010) primarily occupying freshwater habitats.

The family Centrarchidae, which includes the sunfishes, black basses and crappies, is currently placed in the suborder Percoidei and is one of the largest and most diverse suborders in the Perciformes (Johnson 1993). This family, which is endemic to North America, contains eight genera and 34 extant species, and is one of the most morphologically diverse freshwater families on the continent (Cook and Phillip 2009).

The fossil record of the family Centrarchidae is fairly well known, extending from the Late Eocence to Early Oligocene (approximately 35 mya) to the very early Holocene (approximately 10 years ago) (Wilson and Williams 1992, Near et al. 2005).

Records suggest that centrarchids, both fossil and extant species, are found only in North America, indicating that this is the region of origin and diversification for the group (Near et al. 2005).

Cichlids and centrarchids differ in several morphological characteristics. Cichlids have one nostril on each side of the snout (versus two nostrils in centrarchids) and an interrupted lateral line (versus continuous in centrarchids, Figure 1). Centrarchids also have a larger operculum that has an angular posterior margin, which is considered an apomorphic character. Morphological differences exist in the pharyngeal jaw apparatus as well as in the otoliths (Galis and Druker 1996, Gaemers 1984).

This dissertation reports research findings of an interfaunal comparison of functional morphological traits and feeding ecology between Neotropical cichlids and Neartic centrarchids. Morphological approaches have been used extensively to examine species organization, assemblage structure, and patterns of convergence of taxonomic groups, including fishes at intercontinental scales. I used multivariate techniques (Stayton 2006) and morphological approaches based on community trait distribution (Ricklefs and Schluter 1993, Ricklefs and Miles 1994) to identify whether cichlid and centrarchid assemblage structure was correlated with species richness and to infer the ecological factors that are most influential in structuring these assemblages (Chapter II).

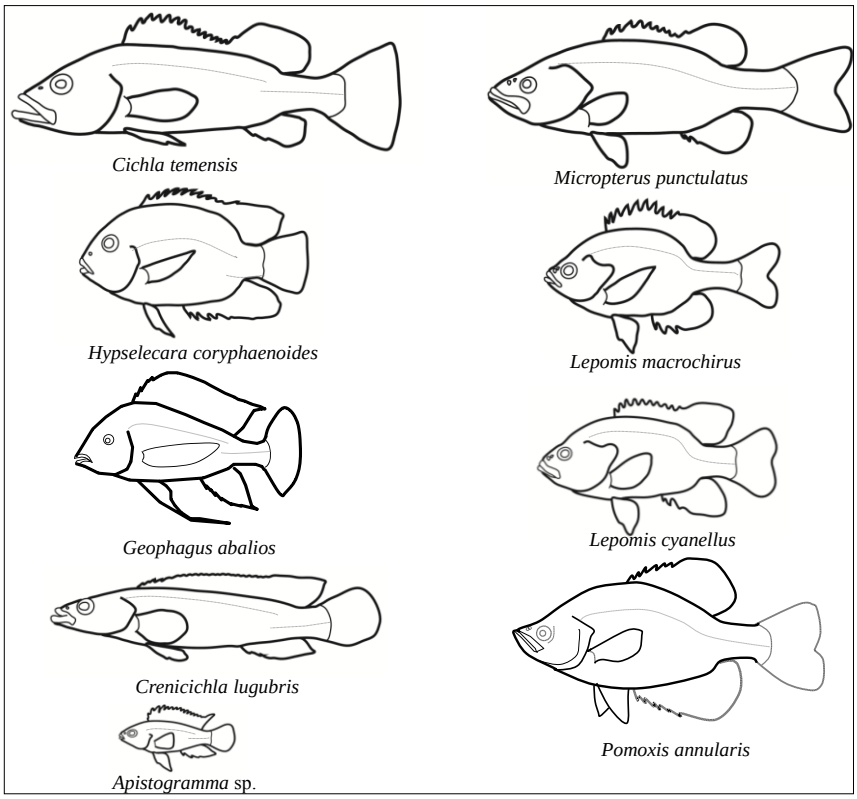


Figure 1. Species revealing shape and relative size variation among representative cichlids and centrarchids used in this study. Centrarchids are in right column and cichlids in the left column.

Ecomorphological studies of freshwater fishes have provided strong evidence for convergent evolution (Marrero and Winemiller 1993, Winemiller et al. 1995, Ruber and Adams 2001, Knouft et al. 2003, Hulsey et al. 2008, Carlson and Wainright 2010). Several species of cichlids and centrarchids have comparable morphologies and similar feeding mechanics (Norton and Brained 1993). Convergence in feeding modes has been described in distantly related perciform species (Norton and Brianerd 1993) as well as in

other teleost fishes (Marrero and Winemiller 1993, Winemiller and Adite 1997). In Chapter III, I examine trophic morphology and diets (based on stomach contents analysis and isotopic data) of cichlids and centrarchids in order to investigate whether fishes in these two perciform lineages reveal one-to-one patterns or morphological and ecological convergence. Convergent evolution in response to similar environmental settings results in organisms with correlated morphologies and trophic niches, thus I expected to observe a pattern in which morphologically similar species overlap in both dietary and isotopic space.

The two chapters outlined above focus on the integration of functional morphology and ecology of perciform fishes to determine the extent to which natural selection drives species in divergent lineages to occupy similar ecological niches. Finally, in Chapter IV, I summarize the findings and highlight the importance of approaches based on functional traits to describe community assembly and structure. I argue that a focus on functional traits enables inferences regarding the role of ecological interactions (e.g., competition, limiting similarity, etc.) as well as the biotic environments (e.g., habitat structural complexity), and that these questions can be addressed across a hierarchy of spatial scales.

CHAPTER II

LOCAL-SPECIES DIVERSITY IN TROPICAL AND TEMPERATE FLOODPLAIN RIVERS: A MORPHOLOGICAL APPROACH

INTRODUCTION

During the last few decades, a large body of ecological research has revealed that patterns of species richness and community organization derive from interactions between local and regional processes (Algar et al. 2011) and constraints set by history and biogeography (Ricklefs and Schluter 1993). Multiple spatial scales have been used to examine species diversity (Levin 1992, Oberdoff et al. 1995, Huston 1999). At a local scale, species richness can be limited by biological interactions, productivity, habitat complexity, and environmental stress (Houston 1999), and coexistence is a function of both niche dimensionality and resource partitioning (MacArthur and Levins 1967). At a large scale (e.g., regional or global), physical factors (e.g., climate) and historical biogeography are major determinants of species richness. Although, local diversity is generally affected by regional-scale processes (Algar et al. 2011), local factors (e.g. biotic and abiotic) are invoked to explain niche patterns and local population dynamics.

Morphological approaches have been used extensively to examine community organization (Pianka and Huey 1978, Ricklefs and Travis 1980, Winemiller 1991), compare assemblage structure between continents (Lamouroux et al. 2002, Inward et al. 2011), explore community assembly rules (Weiher et al. 1998, Moreno et al. 2006), reveal patterns of convergence and divergence (Winemiller et al. 1995, Stayton 2006),

and examine assemblage structure in association with specific habitat features (Willis et al. 2005, Hoeinghaus et al. 2007, Montaña and Winemiller 2010). Early studies based on morphological traits among co-occurring species of vertebrates (Ricklefs and Schluter 1993, Ricklefs and Miles 1994) evaluated patterns of species distribution in assemblage morphological space and the size of this space in relation to species richness (Figure 2). The Niche Compression Model predicts that when new species are added into a community, the total community niche volume (morphological space) should remain relatively constant, while average niche breadth should decline in order to limit niche overlap and competition (Figure 2a-c) (MacArthur 1972). Werner (1977) found that North American sunfishes (*Lepomis* species) with similar niches when occurring alone in lentic habitats will undergo niche shifts and subsequently segregate in niche space on the basis of food size when they occur syntopically (in the same habitat), which supports the idea that food resource competition imposes limits on phenotypic similarity (MacArthur 1972). According to the Niche Expansion Model, community niche volume increases to accommodate new species in an expanded species assemblage, with average niche differences among species remaining relatively constant (Figure 2d-f) (Ricklefs and Miles 1994). Ricklefs and Travis (1980) found that in bird assemblages with increasing levels of diversity, species similarity within morphospace remained relatively constant and species tended to be added to the periphery of morphospace, which supports the niche expansion model. Other studies involving bats (Findley et al.1972), lizards (Ricklefs et al. 1981), and fishes (Gatz 1979, Winemiller 1991) also suggest a general tendency for morphospace to increase with species richness, while the nearest-

neighbor distances within assemblage morphospace tend not to vary with richness. Using populations of three-spine sticklebacks (*Gasterosteus aculeatus*), Bolnick et al. (2010) experimentally tested whether or not ecological release from interspecific competition results in intraspecific niche expansion. Their findings seem to agree with the niche expansion hypothesis (Van Valen 1965) in which release from trout (*Oncorhynchus clarki*) competition increased stickleback population niche width via increased among-individual variation, while individual niche widths remained unchanged.

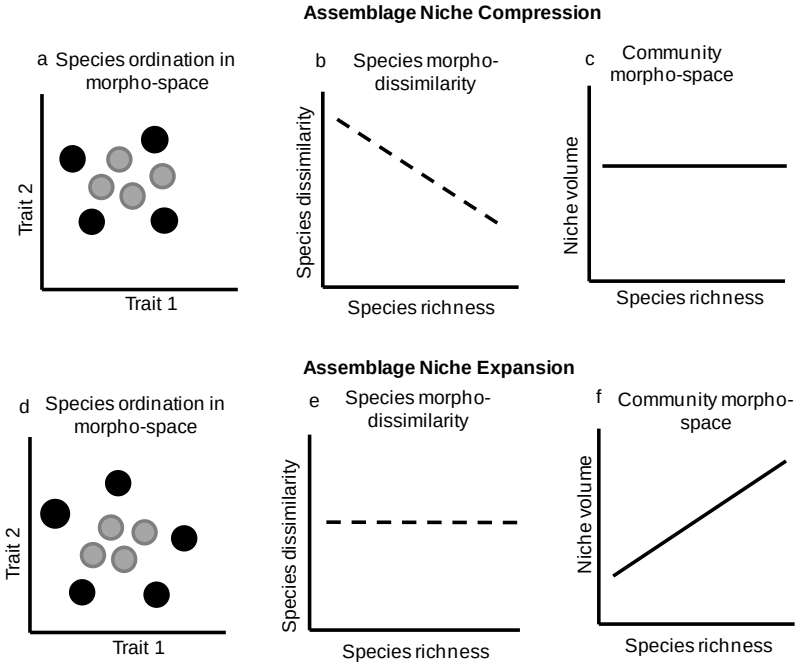


Figure 2. Theoretical models of species distribution in morphological space and the relationships with species richness. Original species in morphological space (grey filled circles), new species added (black filled circles), niche volume (solid lines), species dissimilarities (dashed lines). Under the niche compression model, average differences among species decreases (b) as new species are added assemblage (a), with total morphological niche volume remaining relatively constant (c). Under the niche expansion model, average differences among species remaining relatively constant (f) as new species are added (d), increases is accompanied by an assemblage morphological niche volume (f).

Approaches based on morphological traits have been used to assess the importance of niche filtering or limiting similarity in structuring diverse ecological communities (Mouillot et al. 2007, Ingram and Shurin 2009, Wilson and Stubs 2012). Niche filtering results in assemblages of coexisting species that are more ecologically similar than expected by chance, either because of shared ancestry or evolutionary convergence. In contrast, the limiting similarity model predicts that species with similar traits and ecological requirements will be unable to coexist if resources are limiting, and therefore coexisting species would be expected to be less similar by chance to reduce the negative affect of interspecific competition (MacArthur and Levin 1967). Weiher and Keddy (1995) postulated that limiting similarity should have greater importance at smaller spatial scales, whereas niche filtering should predominate at larger spatial scales. These two models have been investigated as possible mechanisms structuring fish assemblages and have produced variable findings. Schlosser (1987) and Peres-Neto (2004) found that habitat features act as local filters regulating co-occurrence of species that have similar traits. Competition seemed to account for structure of stream fish assemblages in temperate regions (Winston 1995), and predation influenced the structure of fish assemblage at the patch (mesohabitat) scale in tropical (Layman and Winemiller 2004) and temperate (Schlosser 1988) rivers.

Here, I used functional morphology to test ecological theories of species coexistence. Specifically, I examined trait distribution of perciform fishes in assemblage morphological space to evaluate niche relationships. I examined morphological patterns at two spatial scales: macrohabitat (e.g., river channel and floodplain lakes) and

mesohabitat; and did this for two independent perciform lineages that occur in rivers of two continents (South and North America). Specifically, I asked whether or not Neotropical cichlids are more tightly packed in morphospace than temperate centrarchids, and also whether assemblage distributions within morphological space were correlated with species richness across different habitat scales.

I used perciform fishes in the families Cichlidae (South America) and Centrarchidae (North America) as model taxa because of their ecomorphological similarities (Norton and Brainerd 1993) and also because they are diverse and common fishes inhabiting freshwater habitats. The family Cichlidae reveals a particularly high degree of morphological and ecological diversification, with many species often coexisting in the same habitat (Winemiller et al. 1995, Montaña and Winemiller 2010). The family Centrarchidae (sunfishes and basses) is represented by eight genera and 34 species that are morphologically diverse and inhabit freshwater habitats throughout most of North America (Cook and Phillip 2009).

This study was limited to the low-water period. During this period, I expected to find more fishes sharing habitats, because the gradual decent of the water level causes fish density to increase and consequently species interactions should intensify (Lowe-McConnell 1987). I took advantage of multivariate techniques (e.g., principal components analysis) to explore the morphological space occupied by each family within each macrohabitat. Null models were performed and contrasted with observed data to test for statistical differences, and to infer potential ecological factors structuring these assemblages during the low-water period.

MATERIALS AND METHODS

Study sites and field data collection

I conducted this study in four lowland rivers, two in South America (the Cinaruco and the Tambopata) and two in North America (the Neches and the Brazos) (Figure 3). The Cinaruco River is a tributary of the Orinoco River in the Venezuelan llanos of Apure, southern Venezuela (study area approximately located at 6°32´N and 67°24´W). This river has sandy substrates and clear slightly-stained waters, with low pH (Montoya et al. 2006). The Tambopata River drains into the Madre the Dios River in Peru, then becomes the Beni River in Bolivia before it meets its confluence with the Amazon River. The Tambopata carries high loads of suspended sediments of fine grain size, has basic pH, and high turbidity (Barthem et al. 2003). The Neches River in Texas (USA) originates in eastern Van Zandt County, and flows to its mouth at Sabine Lake, an inlet of the Gulf of Mexico. The Brazos River flows 1,485 km from its origin near the Texas- New Mexico border to the Gulf of Mexico. In term of geomorphology, sediments, and water quality, the Neches is more similar to the Cinaruco, and the Brazos is similar to the Tambopata (Figure 3b-e).

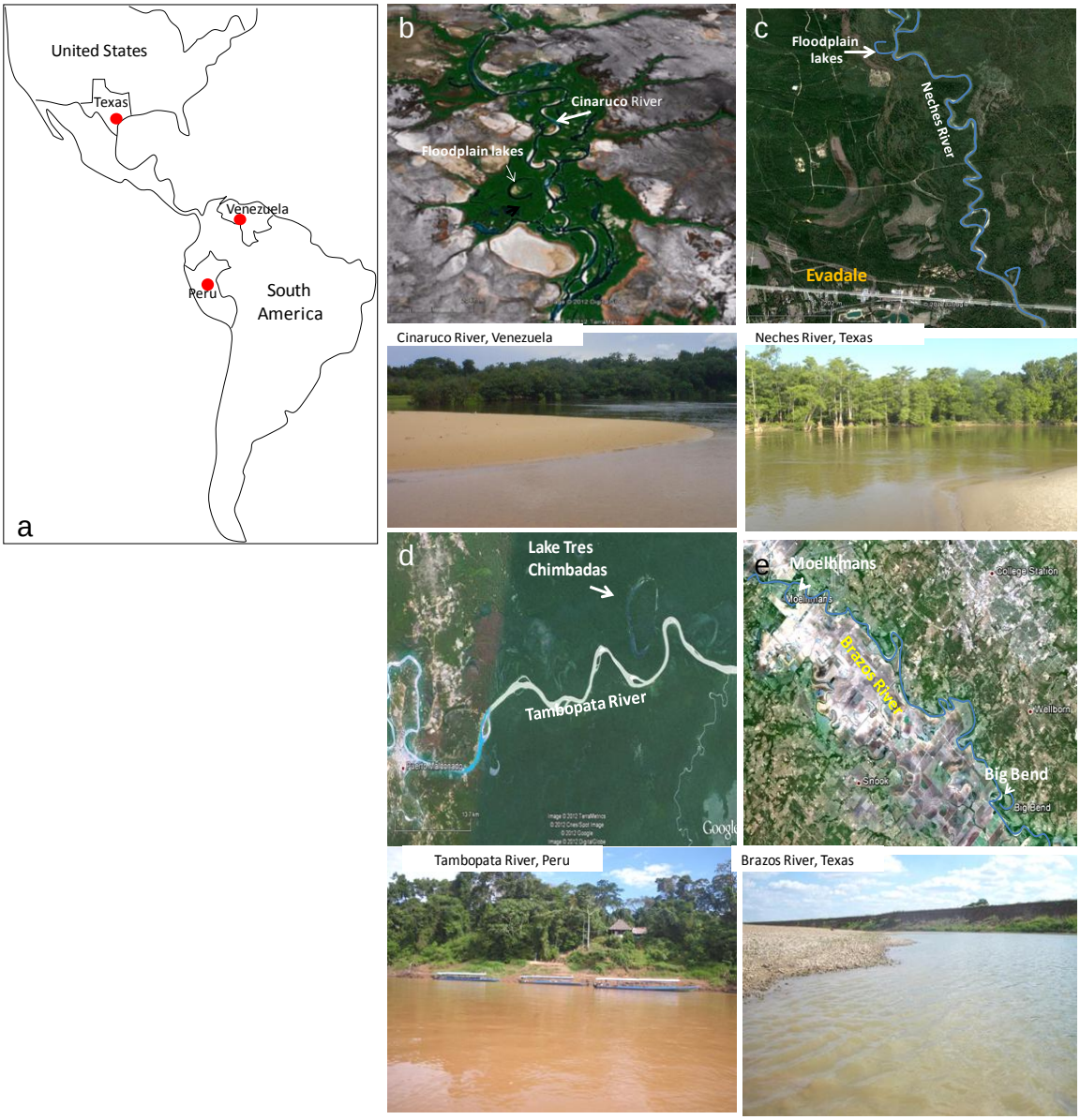


Figure 3. Locations of the study areas in South America and North America (a). The Cinaruco River (b) in Venezuela and Neches River (c) in Texas and the Tambopata (d) in Peru and the Brazos (e) in Texas are meandering floodplain rivers with floodplain lakes associated.

In all four rivers, I conducted field work during the low-water period (defined as the annual dry season in South America and the summer in North America). I conducted field research during the low-water period because I expected to find more fish inhabiting habitats in the littoral zone and to capture them more efficiently. During this season, water levels of the river and floodplains decend, resulting in habitat reduction, higher fish densities, and intensification of many biotic interactions (e.g., predation and competition; Lowe-McConnell 1987). Surveys were standardized to produce fairly accurate and equivalent representation of fish assemblages at similar habitat scales. By 'assemblage', I mean the species and relative abundances of fishes that coexist in a local habitat at a determined time. I sampled fishes from a stretch of the river channel (approximately 20 km) and nearby floodplain lakes (i.e., floodplain lagoons and oxbow lakes). The number of floodplain lakes surveyed varied by river. For instance, in the Cinaruco River, I collected cichlids along the shoreline of seven floodplain lakes, whereas in the Tambopata, only one large, clear-water lake was surveyed (Lake Tres Chimbadas). In the Brazos River, two oxbow lakes, Big Bend and Moehlman's, were sampled, and the main river channel was surveyed approximately 10 km upstream and 10 km downstream from the Texas State Highway 21 bridge. Finally, I surveyed the river channel and two floodplain lakes along the Neches River between the towns Evadale and Spurger (Texas). Habitats were categorized as macrohabitats (floodplain lakes and river channel) and mesohabitats. Four mesohabitats were target for surveys within each macrohabitat, and they were defined based on substrate composition: sand bank (areas with > 95% coarse-sand substrate), leaf litter (areas with > 90% covered by

leaves), rock shoal (areas with > 90% covered by rocks), and submerged wood (areas with > 95 snags or submerged wood).

In the Cinaruco River, I conducted surveys between December of 2005 and May of 2006. In the Tambopata River, I collected during June and July of 2009. In the two Texas rivers, I conducted fish collections during three summers (May to August) from 2009-2011. As a result of the diversity of habitat types in each of the rivers and the logistical difficulties of using certain techniques in the tropical rivers, multiple fishing techniques were necessary in all rivers. Seining was conducted in the Cinaruco, Tambopata, Neches and Brazos rivers within open areas classified as sand banks or leaf litter (seine dimensions: 6.4 x 1.8 m, 4-mm mesh). Baited hooks (#8) were employed in the Cinaruco and the Lake Tres Chimbadas in Tambopata, within habitats with rocky or wooded substrata where seining was inefficient. A cast net (2-m diameter, 1-cm mesh) also was used in leaf litter and wood substrata in Lake Tres Chimbadas in Peru. Electrofishing (pulsed DC from a handled boat unit) was conducted in the two Texas rivers within areas with rocky or wooded substrata. In tropical rivers, 282 mesohabitat samples (669 total seine hauls, 340.8 hours fishing with baited hook, and 130 cast net trows) yielded 8,705 individuals of cichlids. In temperate rivers 241 mesohabitat samples (516 total seine hauls, 7,177 time/seconds of electrofishing) yielded 9,675 individuals of centrarchids. Captured specimens were preserved in a 15% formalin solution in the field and transported to the laboratory where they were examined and measured. Voucher specimens were archived in the Museo de Ciencias Naturales at

UNELLEZ Guanare, Venezuela, and the Texas Cooperative Wildlife Collection at Texas A&M University, Texas, USA.

Morphological traits

For all species collected (26 species of cichlids and 13 species of centrarchids, Table 1), I recorded 23 morphological characters (Table 2) in five adult specimens per species. Traditional morphometric measurements were made using calipers (to nearest 0.01 mm). I chose measurements to reflect various facets of trophic ecology, swimming behavior, and habitat use (Gatz 1979, Winemiller 1991, Willis et al. 2005). Although 23 variables were measured, 21 variables were converted to proportions of standard length, body depth, body width, or head length following Winemiller (1991), so that descriptors of body and fin shape could be analyzed without the influence of body size. Ratios of body size can introduce allometric bias into shape analysis, but allometric influences should be negligible for interspecific comparisons in which a single size class is chosen to represent a given species (Winemiller 1991). I performed preliminary analysis using several techniques to remove the effect of body size on shape (e.g., residual analysis, shearing and analysis of covariance; McCoy et al. 2006), and the results from these methods were virtually identical. Therefore, I used standardized values of selected ratios as descriptors of shape that have straightforward ecological and functional interpretations (Winemiller 1991, Willis et al. 2005).

Table 1. Cichlid and centrarchid species used in this study. Taxonomic classification for the family Cichlidae follows López-Fernández et al. (2010) and for the family Centrarchidae follows Near et al. (2005).

Cichlidae Species	Tribes	Centrarchidae Species	Tribes
Cinaruco River		**Neches River**	
Acaronia vultuosa	Cichlasomatini	*Lepomis cyanellus*	Lepomini
Aquidens diadema	Cichlasomatini	*Lepomis gulosus*	Lepomini
Apistogramma sp.	Geophagini	*Lepomis humilis*	Lepomini
Apistogramma hoignei	Geophagini	*Lepomis macrochirus*	Lepomini
Biotodoma wavrini	Geophagini	*Lepomis miniatus*	Lepomini
Biotecus dicentrarchus	Geophagini	*Lepomis megalotis*	Lepomini
Crenicichla lugubris	Geophagini	*Lepomis microlophus*	Lepomini
Crenicichla aff. *wallacii*	Geophagini	*Micropterus punctulatus*	Micropterini
Geophagus abalios	Geophagini	*Micropterus salmoides*	Micropterini
Geophagus dicrozoster	Geophagini	*Pomoxis annularis*	Archoplitini
Heros sp.	Heroini	*Pomoxis nigromaculatus*	Archoplitini
Hoplarchus psittacus	Heroini	*Centrarchus macropterus*	Centrarchini
Hypselocara coryphaenoides	Heroini		
Mesonauta insignis	Heroini	**Brazos River**	
Satanoperca daemon	Geophagini	*Lepomis cyanellus*	Lepomini
Satanoperca mapiritensis	Geophagini	*Lepomis gulosus*	Lepomini
Cichla intermedia	Cichlini	*Lepomis humilis*	Lepomini
Cichla orinocensis	Cichlini	*Lepomis macrochirus*	Lepomini
Cichla temensis	Cichlini	*Lepomis miniatus*	Lepomini
		Lepomis megalotis	Lepomini
Tambopata River		*Lepomis marginatus*	Lepomini
Aequidens tetramerus	Cichlasomatini	*Lepomis microlophus*	Lepomini
Apistogramma luelingi	Geophagini	*Micropterus punctulatus*	Micropterini
Apistogramma urteagai	Geophagini	*Micropterus salmoides*	Micropterini
Cichlasoma amazonarun	Heroini	*Pomoxis annularis*	Archoplitini
Crenicichla semicincta	Geophagini		
Mesonauta festivus	Heroini		
Satanoperca jurupari	Geophagini		

Data analysis

Analysis of morphospace

To describe the morphological space occupied by each perciform assemblage and examine among-species differences in functional traits, I performed a principal components analysis (PCA) on the matrix of species traits. Species loadings on the dominant axes provided the basis for inter-assemblage comparisons of species distributions in morphological space. Morphological data for 130 specimens of cichlids from the Cinaruco and Tambopata rivers and 120 specimens of centrarchids from the Neches and Brazos rivers were log transformed prior to the analyses to enhance the interpretation of the axes and fulfill assumptions of this multivariate approach. I used a multivariate MANOVA to test for significant differences among spaces occupied by the four perciform assemblages in the morphospace described by PCA.

Because the measurements of morphological traits made on five adult specimens of a given species were highly consistent, I calculated the species means for the 23 morphological attributes. These means were then used for PCA to ordinate species in morphospace and to calculate Euclidean distance among species based on species loadings on the first four PCA axes. I weighted the Euclidean distance between each pair of species using the proportion of variance explained by each axis as the weighted factor (w). I computed the squared differences between variables (unstandardized Euclidean distance, $d_{(j,k)} = [\Sigma^n (x_{ij} - x_{ik})]^{1/2}$, where $d_{(j,k)}$ was the distance between species j and k, and x_{ij} and x_{ik} were the character loadings on the same PC axis for the species pair j and k on their original scales and then multiply these squared differences by the corresponding

weights. The weighted Euclidean distance was performed by the following formula: $d_{(j,k)} = \text{sqrt}[\Sigma^n w_i(x_{ij} - x_{ik})^2]$, where n was the number of attributes, x_{ij} and x_{ik} were standardized values of the same character for the species pair j and k, and w_i was a weight attached to attribute i.

From the pairwise Euclidean distance calculations, I determined morphological measures of mean nearest neighbor distance (NND), an index of species packing in morphological space, the standard deviation (SD) of NND, an index of evenness of species dispersion or packing in morphological space, and the average distance to the assemblage centroid (CD), an index that provides an estimate of the relative size of the morphological hypervolume or total niche space occupied by an assemblage (Winemiller 1991, Montaña andWinemiller 2010). Lower values of SD NND indicate that species are more regularly or evenly dispersed in morphospace, and this pattern would be consistent with the theory of limiting similarity (MacArthur and Levin 1967, Ricklefs and Trevis 1980). I performed simple linear regressions using SPSS 15.0 for Windows (2007) to test the relationship between species richness and mean NND, as well as SD NND and mean CD. Because these indices were calculated for each mesohabitat type within major macrohabitats, I compiled sub-matrices containing species from individual mesohabitat samples for each river.

Morphological null model

To test the hypothesis that assemblage morphological structure differs from random expectations when viewed at different spatial scales, I used a program that generates random species assemblages drawn from the observed species pool and calculates the nearest neighbor distances (NND) and centroid distances (CD). The input to the program was an *n*-by-4 matrix consisting of the first four PCA axes for each species in an *n*-species assemblage. The proportion of the variance modeled by each PCA axis was used as input to compute weighted Euclidean distances.

For each species assemblage, the program repeatedly generated random samples of *k* rows from the *n* rows representing the species in the assemblage matrix and computed the nearest neighbor distances (NND) and centroid distances (CD) for the sampled rows. For smaller assemblages, such as the Brazos (11 species) and Tambopata (7 species), the program generated all possible combinations (samples) of *k* rows from the original *n*. For large assemblages such as in Cinaruco (n = 19 species), the program generated 1000 random samples of size *k*.

The observed values for mean of NND, standard deviation of NND, and mean CD from natural assemblages were compared against the randomly generated sets of species trait distributions containing the same number of species as the real assemblage via standard linear regressions using SPSS 16.0 (2007). The randomly generated null distributions were necessary because standard statistical comparisons of morphological Euclidean distances can be biased when the numbers of species in two assemblages are unequal. I used Fisher's test of combined probabilities ($\chi^2 = -2\ \Sigma\log(Pi)$) to test whether

morphological patterns from each mesohabitat type were significantly different from those drawn randomly from the set of species pools. The Fisher's chi square summation test (Sokal and Rohlf 1995) combines probabilities (*Pi*) from all samples within a set of related comparison to determine if the overall differences between observed versus random values is statistically significant. Finally, I performed an analysis of covariance (ANCOVA) using SPSS 16.0 (2007) to test for differences in regression slopes and intercepts of observed and randomly generated datasets. The homogeneity of regression (slope) assumption was tested to evaluate the interactions between the covariate (e.g., species richness) and the independent variable (e.g., observed vs. random values of morphological indices, including the mean and standard deviation of NND and the mean CD).

RESULTS

For both cichlid and centrarchid assemblages, the number of species was higher in relatively heterogeneous littoral habitats (e.g., submerged wood, leaf litter, and rock shoals) of floodplain lakes than the same habitats in the river channel (Table 2). In the Cinaruco, cichlids were common in both the river channel and floodplain lakes, with only two species restricted to specific macrohabitats. *Cichla intermedia* was restricted to structurally complex habitats of the river channel, and *Satanoperca mapiritensis* only occurred in floodplain lakes. Surveys in the Tambopata River channel did not yield cichlid species. Seven species of cichlids were collected from the connected floodplain lake Tres Chimbadas in the Tambopata. The Neches and Brazos rivers shared similar

species of centrarchids with the exceptions of two species, *Centrarchus macropterus* and *Pomoxis nigromaculatus*, which were present only in the Neches River. Centrarchids seemed to be more abundant in littoral habitats of the Neches than in same types of habitat of the Brazos.

Table 2. Ranges of species richness for perciform species assemblages captured from mesohabitats in floodplain lakes and channel macrohabitats of four rivers.

Macrohabitat	Mesohabitat	Cinaruco	Tambopata	Neches	Brazos
Floodplain lake	Wood	4 - 9	3 - 5	4 - 8	4- 8
Floodplain lake	Leaf litter	4 - 12	3 - 5	5 - 9	3 - 8
Floodplain lake	Rock	4 - 8			
Floodplain lake	Sand bank	3 - 12			
Channel	Wood	3 - 5		3 - 9	3 – 7
Channel	Leaf litter	4 - 8			
Channel	Rock	4 - 9		4 - 7	3 – 6
Channel	Sand bank	4 - 7		3 - 7	3 – 7

Morphologically, species were separated on the basis of head and body shape, mouth width and position, and fin dimensions. The PCA performed on functional morphological traits resulted in four axes (PC1- 4) explaining 68.73% of the total variation (Table 3). The first two PC axes modeled more than half of the variation in morphology (approximately 51.4%). PC1 described a gradient that reflected differences in morphological traits mostly associated with locomotion, such as body size and shape, and fin dimensions. Species with positive scores on PC1 had relatively deep and laterally compressed bodies and short snouts (e.g., sunfishes and heroine and cichlasomatine cichlids). Negative values on PC1 were associated with large mouths and large dorsal and anal fins, features possessed by *Cichla* spp. and *Crenicichla lugubris* (Cichlidae) as well as *Micropterus* spp. and *Pomoxis* spp. (Centrarchidae).

PC2 was mostly associated with traits involved with feeding, revealing a gradient strongly influenced by head height, eye diameter, eye position, snout length, and body depth. Species with large positive scores on PC2 had elongated bodies, long and dorso-ventrally compressed heads (e.g., *Crenicichla* spp.), and terminally to dorsally positioned mouths and short snouts (e.g., *Apistogramma* spp. and *Biotoecus*).
High negative scores on PC2 were associated with laterally-compressed bodies, long and high dorsal fins (e.g., *Lepomis* spp.), large eyes, and broad heads (e.g., *Pomoxis* spp.).

The MANOVA performed on the assemblage PCA coordinates for the four floodplain rivers confirmed that based on functional morphological traits, species occupied significantly different areas within the total morphospace ($df_{3,48}$, $F = 4.56$, $p < 0.0001$). The Mantel test revealed high correlation between morphological structure of

local species assemblages and habitat types ($r = 0.10$, $p = 0.04$) suggesting an association between functional traits and mesohabitats.

Table 3. Eigenvalues, percentage variation modeled, cumulative variation and morphological variable loadings for PC axes 1-4 from analysis of 19 cichlids from the Cinaruco River, 7 cichlids from the Tambopata floodplain lake, 12 centrarchids from the Neches River, and 11 centrarchids from the Brazos River.

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	5.54	2.66	1.49	1.27
% of variation	34.74	16.69	9.35	7.98
Cumulative variation	34.74	51.43	60.78	68.77
Head length	-0.03	0.13	0.04	-0.03
Head height	0.21	-0.57	0.10	0.10
Interorbital distance	-0.53	-0.13	-0.23	0.25
Eye position	-0.08	0.49	-0.01	0.18
Eye diameter	0.47	-0.11	0.14	-0.01
Snout length, mouth shut	-0.35	-0.48	-0.19	0.36
Snout length, mouth open	0.61	0.31	0.83	0.56
Maximum body depth	-0.59	0.40	-0.12	0.13
Maximum body width	-0.17	0.14	0.07	0.08
Caudal peduncle depth	0.16	-0.21	0.21	-0.10
Caudal peduncle width	0.46	0.34	-0.13	-0.03
Body depth below midline	0.40	0.15	-0.10	-0.29
Mouth position	0.35	0.09	0.09	0.33
Mouth or gape width	0.43	0.01	0.06	0.25
Dorsal fin length	-0.25	-0.30	-0.30	0.06
Dorsal fin height	-0.69	-0.48	0.40	-0.35
Anal fin length	-0.67	0.29	0.13	-0.30
Anal fin height	-0.83	0.10	0.05	0.22
Caudal fin length	-0.51	-0.20	0.39	-0.11
Caudal fin height	-0.33	0.50	-0.20	0.16
Pectoral fin length	-0.55	0.05	-0.02	0.24
Pectoral fin height	-0.72	0.71	0.25	-0.20
Pelvic fin length	-0.67	-0.28	0.08	0.19

Morphological similarity – species richness

Between-river comparisons

Overall decline in mean NND indicated an increase in species similarity within perciform assemblages in mesohabitats of both tropical and temperate rivers (Figure 4a). This negative relationship (slope: y = -0.02) was statistically significant (r = 0.65, p = 0.02) for the Cinaruco River, but not for the temperate rivers (Neches: r = 0.27, p = 0.52 and Brazos: r = 0.53, p = 0.18), apparently due to low sample sizes for the latter. In the Tambopata floodplain lake, mean NND tended to decrease with increasing species richness, but this relationship was not statistically significant (r = 0.62, p = 0.52) due to small sample size (Figure 4a).

For all four rivers, analysis of total assemblage morphological niche volume measured by mean CD showed a general trend total niche volume to decline slightly with increasing species richness (Figure 4b). Regression slopes were low and negative for all four rivers: Cinaruco (y = -0.01, p = 0.03), Neches (y = -0.03, p = 0. 004), Brazos (y = -0.01, p = 0.04), and the Tambopata River (y = -0.06, p = 0.44). Mean values of CD were greater for cichlid assemblages from mesohabitats in the Cinaruco, a species-rich tropical river (mean CD = 0.61), than for assemblages in mesohabitats of the two temperate rivers, the Brazos and the Neches (mean CD = 0.47 and 0.34, respectively). This suggests that during the low-water period, cichlids from the Cinaruco comprise a larger morphological volume, perhaps as a result of competitive interactions.

For the four rivers, overall evenness of species distribution in assemblage niche space indicated by SD NND increased with increasing species richness in mesohabitats. Regression slopes of SD NND in relation to species richness of mesohabitat samples were low and negative for all four rivers (Appendix A), suggesting a more regular spacing of species dispersion within assemblage morphospace when species richness was greater. Correlations of SD NND with the number of species was statistically significant for the Cinaruco ($r = 0.70$, $p = 0.01$) and Brazos ($r = 0.92$, $p = 0.001$) rivers, but not for assemblages in the Neches and Tambopata rivers (Figure 4b; $r = 0.78$, $p = 0.15$ and $r = 0.78$, $p = 0.66$, respectively).

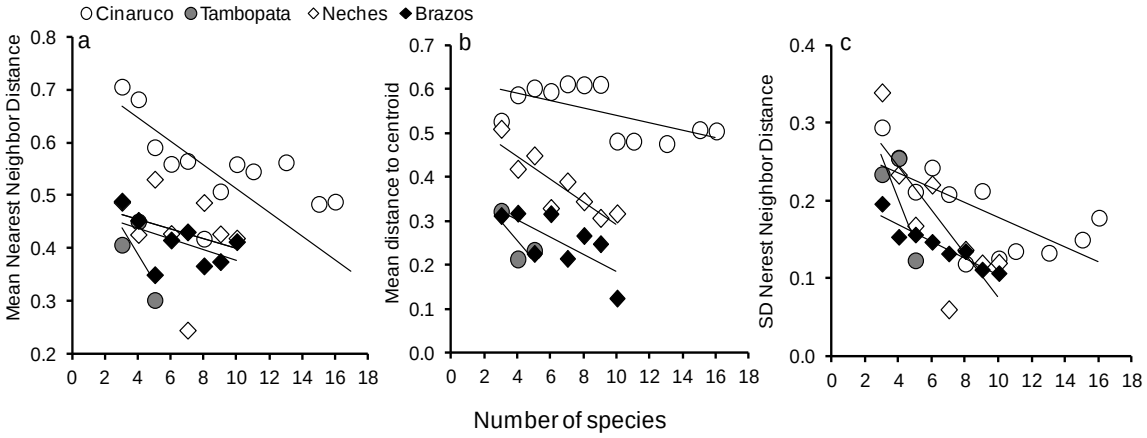


Figure 4. Mean values of morphological dispersion indices (NND, CD, SD NND) computed across multiple mesohabitats assemblages for each observed value for species richness for each river. Linear regressions were statistically significant for the Cinaruco NND (4a), the Cinaruco SD NND (4b) and Brazos (4b). Open dots = mesohabitat assemblages in the Cinaruco, filled dots = mesohabitat assemblages in Tambopata, open diamonds = mesohabitat assemblages in the Neches, and filled diamonds = mesohabitat assemblages in the Brazos.

Local-scale (mesohabitats) comparisons

Results from comparisons of observed data with random generated data from null models indicated nonrandom distributions within morphological niche space of perciform assemblages within mesohabitats, and these patterns are consisting with niche partitioning in response to competition. The χ^2 analysis (observed vs. randomized data) indicated that nineteen of 20 mesohabitat assemblages exhibited mean NND significant greater than those derived from randomizations (Table 4). The NNDs of assemblages of most mesohabitats in most rivers plotted above the mean and 95% confidence interval for the corresponding randomly created assemblages (Figure 5a). These findings suggest that species are less similar within local assemblages than expected by chance, with the only exception being the centrarchid assemblages on sandbank habitats in the channel of the Neches River (Table 4).

Regression slopes for mean NND in relation to species richness for floodplain lakes were low and negative with the exception of Lake Tres Chimbadas (Tambopata) (Appendix A). Mesohabitats in the river channel of the Cinaruco, Neches, and Brazos rivers showed a general pattern of decreasing morphological similarity when adding species to local assemblages (negative slopes for regressions of mean NND versus species richness) (Figure 5a), but this relationship was only statistically significant for rock shoal and wood habitats in the Cinaruco and Neches rivers, and sand banks in the Neches (Table 4).

Regression slopes of CDs were low and positive for perciform assemblages in mesohabitats of the Cinaruco River (Figure 5b), but low and negative for assemblages in

the Tambopata floodplain lake and for most temperate assemblages (Appendix A). Fisher's summation χ^2 indicated that assemblages in the Cinaruco are significantly more dispersed in morphological niche volume than expected at random (Table 4), which tends to support the niche expansion model. Mean CD values were smaller for centrarchid assemblages (ranging between 0.33 - 0.41 in the Neches and 0.19 - 0.31 in Brazos) when compared with cichlids (ranging between 0.42 - 0.57 in the Cinaruco).

With few exceptions, results from the assemblage structure measures (NND and CD) provided support for the niche expansion model (Table 5) for both cichlid and centrarchid assemblages at the local mesohabitat scale. Support for the niche expansion model was demonstrated by mean NND values larger than expected at random, regression slopes for mean NND in relation to species richness of observed assemblages that were greater or not significantly different than random assemblages, and statistically significantly greater slopes for mean DC in relation to species richness of observed compared to randomly generated assemblages (Table 5). The niche compression model was support by findings for centrarchid assemblages in wood patches in the main channel of the Brazos River, and four mesohabitat samples yield inconsistent results with regard to the two community niche models (Neches channel -wood and sandbank, Brazos channel – rock shoal, Tambopata lake – wood).

Evenness of species distribution (measured by SD NND) varied according to habitat type (Table 4). In the Cinaruco, six of eight mesohabitats had perciform assemblages that were less evenly dispersed within morphological niche space than expected at random (e.g., χ^2 of observed values were significantly greater than random

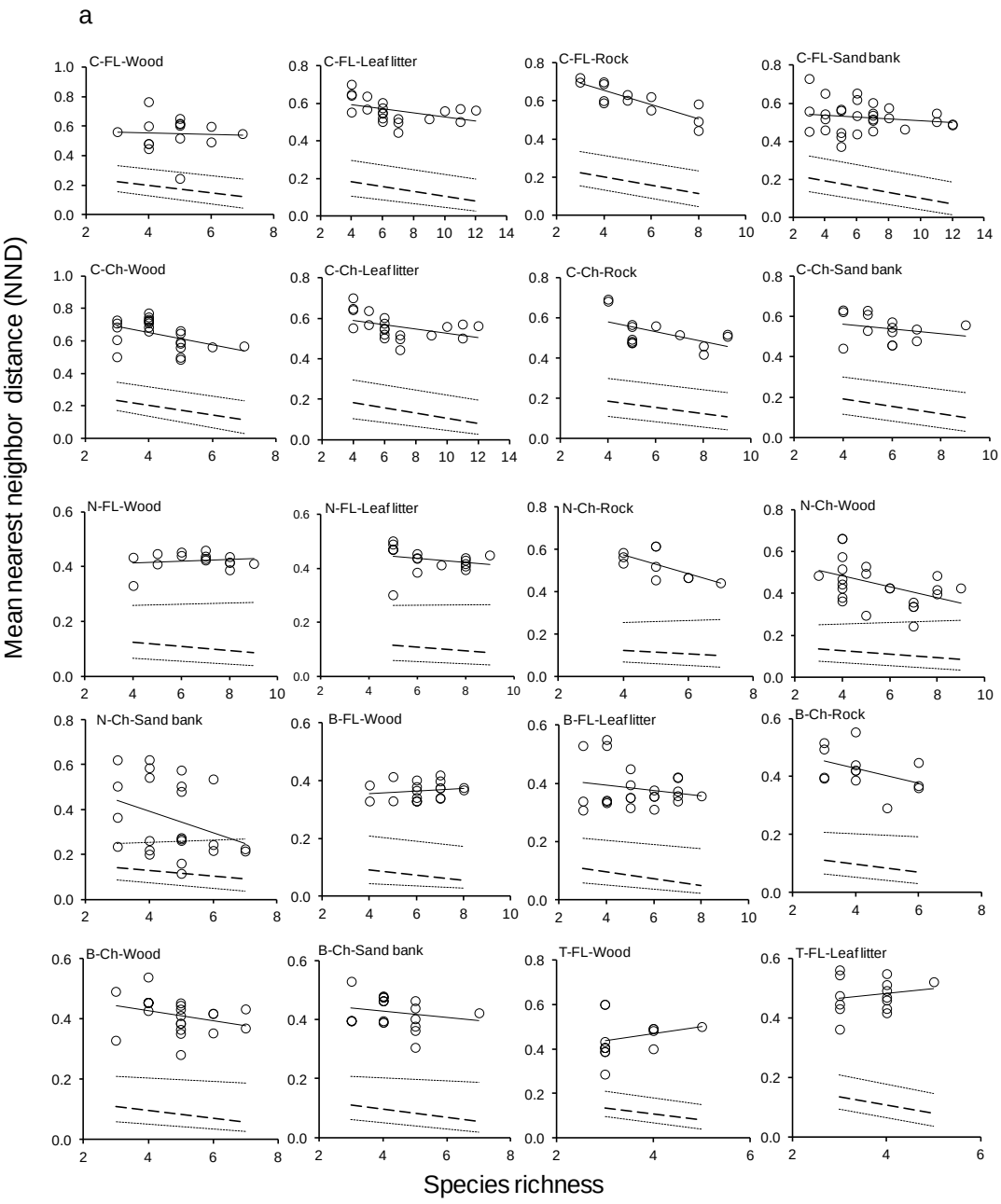
expectation). In the two temperate rivers, Neches and Brazos, four of 10 mesohabitats revealed dispersion of species within morphological niche space (Table 4) than was less even than expected at random.

The general trend was for SD NND to remain relatively constant or decline when species richness increased (Figure 5c), but this pattern was statistically significant only for rock shoal habitats in the Cinaruco ($r = 0.76$, $p = 0.003$) and submerged wood in the river channel of the Neches ($r = 0.49$, $p = 0.02$) (Appendix A). ANCOVA revealed significant differences in regression slopes of SD NND for three assemblages of the Cinaruco River, one assemblage in the Neches River, and three assemblages in the Brazos River when compared with randomly generated assemblages (Table 3). With the exception of assemblages inhabiting leaf litter habitats in floodplain lakes in the Cinaruco, Neches and Brazos rivers, wood habitats in Cinaruco and Neches rivers, and sand banks in the Neches, the observed slopes of most assemblages were greater than the slopes of corresponding randomly generated assemblages (Figure 5b), suggesting that species assemblages are not more evenly dispersed within morphological space with increasing species richness.

Table 4. Results of Fisher's summation chi square (χ^2) for combined probabilities for overall significance ($p < 0.05$) of differences between observed versus randomly generated samples from each of the twenty perciform assemblages in mesohabitats of tropical and temperate floodplain rivers; *p*-values derived from ANCOVA testing for differences between regression slopes of observed and randomly generated assemblages for morphological variables in relation to species richness.

			Mean nearest-neighbor distance		Mean distance to centroid		Standard deviation nearest neighbor distance	
River	Macrohabitat	Habitat category	χ^2 p-values Obs vs. random	Regression slope p-values	χ^2 p-values Obs vs. random	Regression slope p-values	χ^2 p-values Obs vs. random	Regression slope p-values
Cinaruco	Floodplain lake	Wood	< 0.001	0.33	<0.001	0.19	0.1	0.15
	Floodplain lake	Leaf litter	< 0.001	0.02	0.05	0.98	0.02	0.14
	Floodplain lake	Rocks	< 0.001	0.009	<0.001	0.22	0.1	0.03
	Floodplain lake	Sand bank	< 0.001	0.001	0.01	0.19	0.05	0.04
	Channel	Wood	< 0.001	0.17	<0.001	0.42	0.01	0.62
	Channel	Leaf litter	< 0.001	0.04	0.01	0.66	0.01	0.28
	Channel	Rocks	< 0.001	0.02	<0.001	0.02	0.001	0.01
	Channel	Sand bank	< 0.001	0.58	0.01	0.78	0.02	0.26
Neches	Floodplain lake	Wood	< 0.001	0.88	0.5	0.77	0.9	0.73
	Floodplain lake	Leaf litter	< 0.001	0.12	0.9	0.69	0.9	0.53
	Channel	Rocks	< 0.001	0.11	0.1	0.12	0.01	0.09
	Channel	Wood	0.05	0.03	0.9	0.24	0.9	0.02
	Channel	Sand bank	0.99	0.05	<0.001	0.07	0.9	0.84
Brazos	Floodplain lake	Wood	<0.001	0.001	0.97	0.73	0.9	0.01
	Floodplain lake	Leaf litter	<0.001	0.001	0.97	0.29	0.97	0.03
	Channel	Rocks	<0.001	0.001	0.97	0.88	0.5	0.04
	Channel	Wood	<0.001	0.03	0.97	0.53	0.5	0.21
	Channel	Sand bank	<0.001	0.001	0.5	0.21	0.9	0.59
Tambopata	Lagoon	Wood	<0.001	0.61	<0.001	0.51	0.9	0.69
	Lagoon	Leaf litter	<0.001	0.68	0.5	0.66	0.9	0.52

Figure 5. Local mesohabitat comparisons of assemblage morphological patterns in relation to species richness. a) Mean nearest neighbor distance in natural perciform assemblages in the Cinaruco, Tambopata, Neches, and Brazos rivers, b) Mean distance to centroid, and c) Standard deviation of NND. Distances between species in the morphospace were plotted as a function of number of species. Open circles represent observed data, solid lines represent mean of observed data, thick dashed lines represent mean of the randomly generated assemblages, and thin dashed lines represent 95% confidence intervals for random assemblages. Each circle represents compiled samples containing individual species for each habitat type. The Cinaruco River (C) in Venezuela, Neches River (N) in Texas and the floodplain Lake Tres Chimbadas in the Tambopata River (T) in Peru are clearwater systems, and the Brazos River (B) Texas is a river with turbid waters. Cichlids were absent in the mainstem of the Tambopata River. F = floodplain lake, Ch = river channel.


a
C-FL-Wood
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N-Ch-Sand bank
B-FL-Wood
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Mean nearest neighbor distance (NND)
Species richness

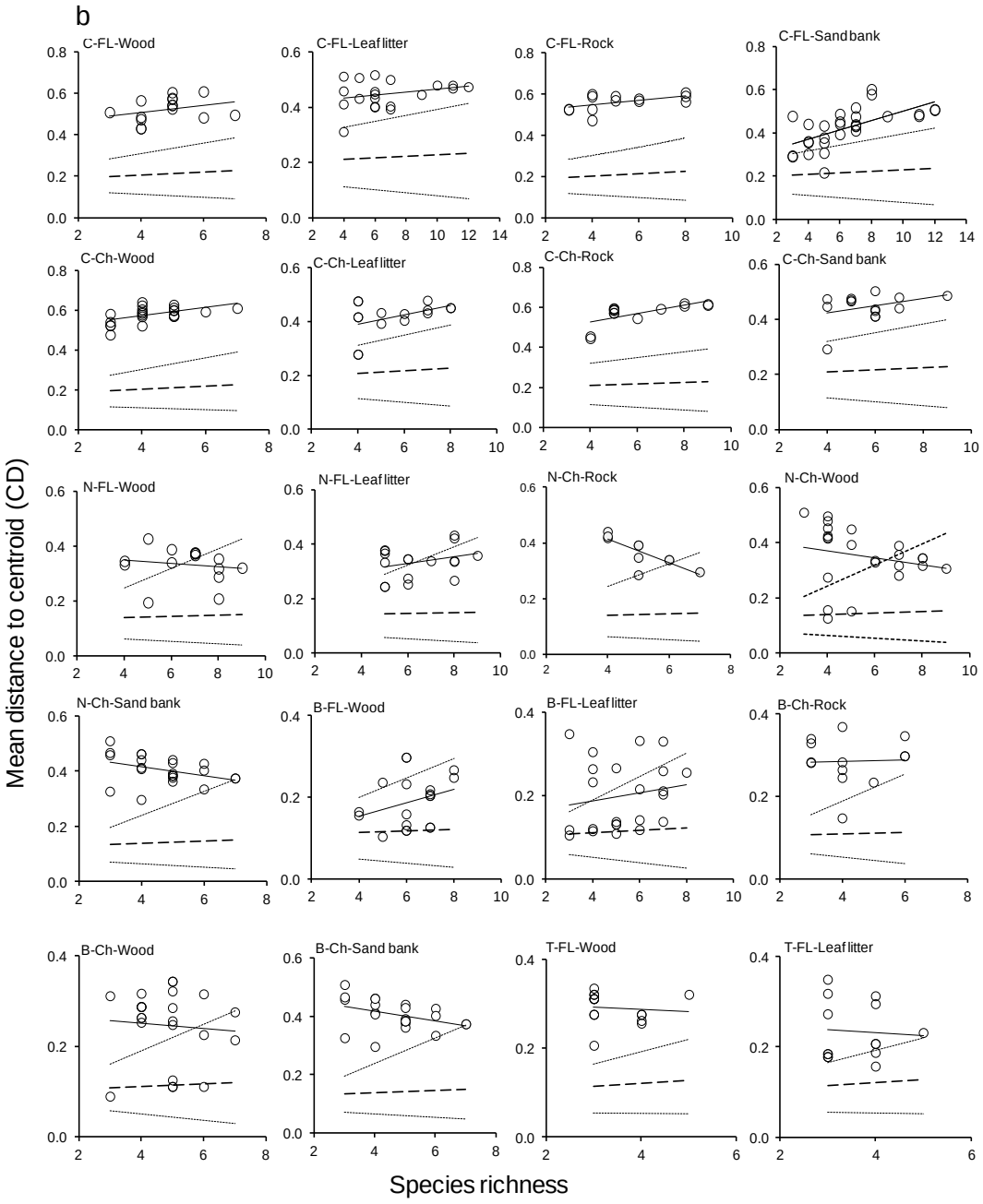

Figure 5. Continued

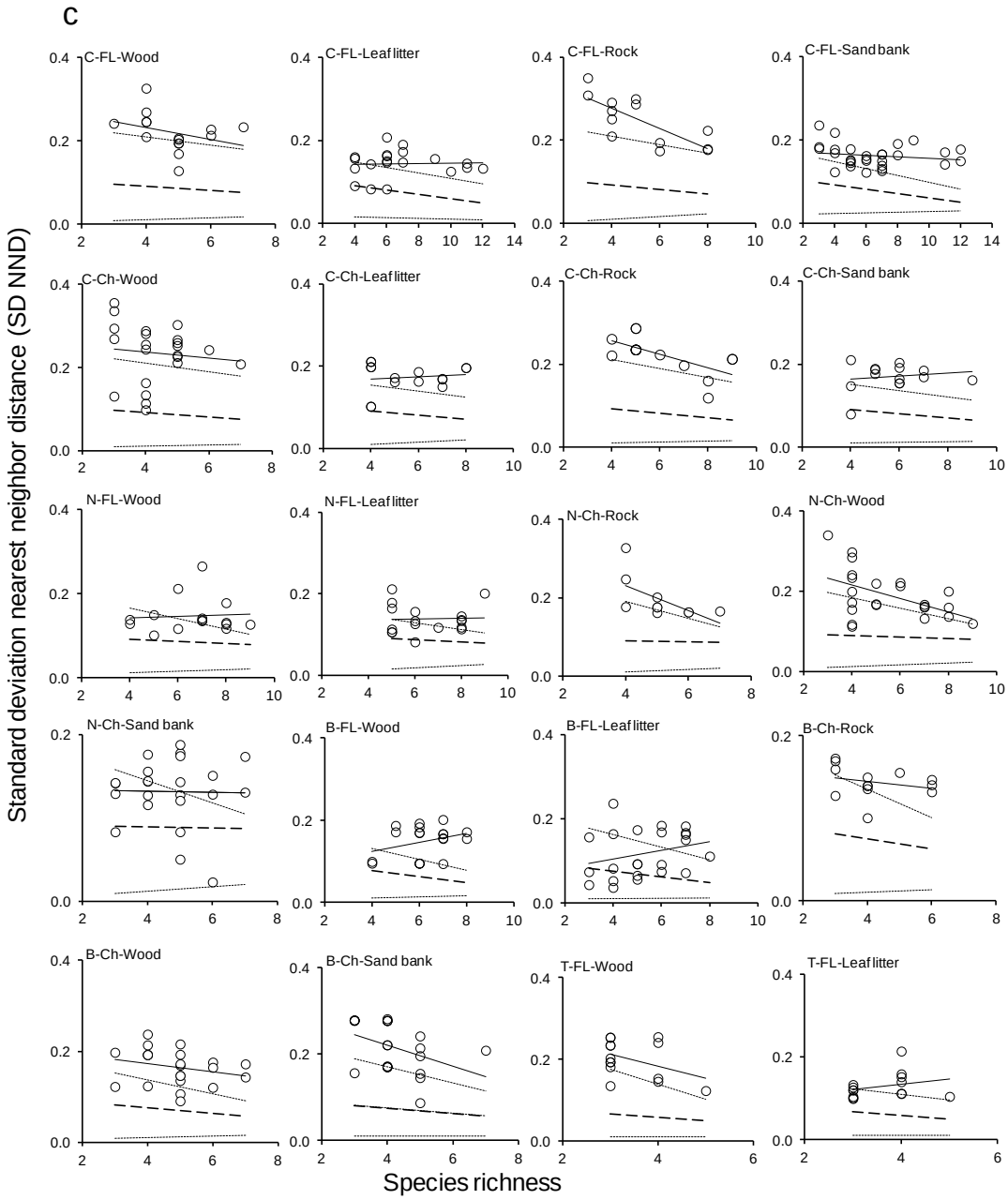

Figure 5. Continued

Table 5. Summary of support for alternative models for niche relationships in relation to increasing species richness of perciform assemblages from mesohabitats of tropical and temperate rivers. If the regression slope for nearest neighbor distance in niche space (mean NND) had had a statistically greater slope than expected at random or a nonsignificant difference relative to random expectation, then the niche expansion model was supported. If the regression slope for mean NND had had a statistically lower slope than expected at random, the niche compression model was supported. If the regression slope for distance to the assemblage centroid in niche space (mean CD) had had a statistically greater slope than expected at random, then the niche expansion model was supported; if the regression slope for mean CD had had a statistically lower slope than expected at random or a nonsignificant difference relative to random expectation, the niche compression model was supported. Increased evenness of species dispersion in niche space with increasing species richness was supported by negative trends and significantly lower regression slopes for SD NND than expected at random. Check mark (√) means support for the model.

			Nearest-neighbor distance in niche space		Size of niche volume		Evenness of dispersion in Niche space
River	Macrohabitat	Habitat category	Compression	Expansion	Compression	Expansion	
Cinaruco	Floodplain lake	Wood		√		√	
	Floodplain lake	Leaf litter		√		√	
	Floodplain lake	Rocks		√		√	
	Floodplain lake	Sand bank		√		√	√
	Channel	Wood		√		√	
	Channel	Leaf litter		√		√	√
	Channel	Rocks		√		√	
	Channel	Sand bank		√		√	
Neches	Floodplain lake	Wood		√			
	Floodplain lake	Leaf litter		√		√	
	Channel	Rocks		√		√	√
	Channel	Wood		√	√		√
	Channel	Sand bank		√	√		
Brazos	Floodplain lake	Wood					
	Floodplain lake	Leaf litter					
	Channel	Rocks	√			√	
	Channel	Wood	√		√		√
	Channel	Sand bank		√	√		√
Tambopata	Floodplain lake	Wood		√	√		
	Floodplain lake	Leaf litter		√		√	

DISCUSSION

In the present study, I analyzed patterns of local perciform assemblage organization with respect to morphological attributes. Morphological analyses derived from observed versus randomized datasets yielded means and standard deviations of nearest neighbor distance and mean distance from the centroid in morphological space yielded similar pattern in cichlid and centrarchid species assemblages. In all but one of twenty cases that were examined, observed assemblages were significantly more dispersed within assemblage morphological space than predicted at random. In general, cichlids in the species-rich Cinaruco River were generally more dispersed within assemblage morphospace than cichlids in the floodplain lake of the Tambopata River and centrarchids in channel and floodplain lake habitats of two temperate rivers. The observation that species within real assemblages were significant less similar than compared to those in randomly generated assemblages supports the idea that local assemblages are organized by competitive interactions.

When regression slopes were compared between observed assemblages and random assemblages drawn from the regional species pool for mean nearest-neighbor distance and distance from centroid, most cases supported the niche expansion model, and few cases supported the niche compression model. The niche expansion model was strongly supported for cichlid assemblages in the species-rich Cinaruco River, centrarchid assemblages in leaf litter and rock habitats in the Neches River, centrarchid assemblages in rock habitats in the main channel of the Brazos River, and leaf litter habitats in Lake Tres Chimbadas in the floodplain of the Tambopata River.

Analyses based on species scores on four morphological gradients showed that both cichlid and centrarchid assemblages display high morphological diversity for traits inferred to be associated with important niche dimensions (e.g., use of habitats and food resources). These independent lineages have evolved similar affinities for relatively shallow and/or lentic habitats of river channels and floodplains. During the low-water period, there was high overlap in cichlid and centrarchid assemblage structure at the scale of mesohabitats, even though species richness often differed. In the Cinaruco River, species richness among mesohabitats varied between eight species in wood to fourteen species in leaf litter and sand banks. Species richness in mesohabitats of the Neches and Brazos rivers varied between eight in rocks and sand banks to ten species in leaf litter and wood. The main channel of the Tambopata River yielded no cichlids, but the assemblage composition in the floodplain lake yielded three to five cichlid species in leaf litter and submerged wood mesohabitats.

A limited number of environmental factors may determine habitat use by cichlids and centrarchids. The apparent absence of cichlids in the Tambopata River channel can be explained by high concentrations of suspended sediments that made the water turbid, which impairs visually mediated activities in cichlids (Lowe-McConnell 1987). Similarly, centrarchid species richness and abundance was higher in littoral habitats of the Neches River channel than the same type of habitat of the Brazos River, suggesting that the high turbidity of the Brazos negatively affects these fishes (Gardner 1981). Substrate heterogeneity and composition also was associated with spatial distributions of cichlids and centrarchids. For example, dwarf cichlids, including *Apistogramma* spp. and

Crenicichla aff. *wallacii*, were most abundant in leaf litter habitats. Geophagine cichlids that winnow fine substrates to extract aquatic invertebrates (*Geophagus* spp. and *Satanoperca* spp.) were more common in sandbank habitats. Piscivorous cichlids (e.g., *Cichla* spp.) tended to be associated with structurally complex substrates. Jepsen et al. (1997) found that sympatric *Cichla* species in the Cinaruco River subdivided habitat and food resources. *Cichla intermedia* differed from its two congeners by occurring nearly exclusively in areas of the river channel with moderate to swift current velocities near structures, whereas *C. orinocensis* was more common along the shorelines of lagoons and in shallow lentic habitats of the river channel. *Cichla temensis* occurred in a greater range of habitats in lagoons and the river channel, but larger individuals usually occupied deeper waters where neither of its congeners occurred. During the low-water period, Jepsen et al. (1997) also found that *C. temensis* consumed larger prey, and *C. orinocensis* and *C. intermedia* consumed different proportions of small prey taxa.

Centrarchids also segregated according substrate types and water depth. Many *Lepomis* species, for example, were captured in shallow areas with submerged leaf litter or woody debris, whereas larger piscivores such as *Micropterus* spp. occupied areas of the river channel that contained structures with less density and complexity. Habitat segregation by centrarchids has been shown to be associated with resource availability (Werner 1977, Werner and Hall 1977) and size-dependent threat of predation (Hall and Werner 1977).

Tropical fish assemblages are known to exhibit higher levels of niche diversification than those from similar habitats in temperate regions (Winemiller 1990).

In this study, I found that tropical cichlids and temperate centrarchids exhibited a significant tendency toward morphological niche expansion in relation increasing species richness within local habitats. Niche expansion has been interpreted as evidence that competition influences community structure (Ricklefs and Travis 1980, Wieher et al. 1998) and can arise from greater dietary, morphological, and behavioral diversity, to name only a few factors. Tropical cichlid and temperate centrarchid assemblages appear to be influenced by biotic interactions during the low-water periods in natural fluvial systems. In tropical regions, for example, the annual dry season is associated with resource limitation for most fishes (Lowe-McConnell 1987), although piscivores may have greater food availability in shrinking aquatic habitats (Jepsen et al. 1997, Rodriguez and Lewis 1997). The magnitude of biotic interactions structuring temperate fish assemblages are perhaps affected by less predictable hydrological regimes (Winemiller et al. 2000, Zeug and Winemiller 2008). In the Brazos River, for example, variation in flood events results in different frequencies of flood connections in floodplain lakes (oxbows), and flood timing favors colonization and persistence of certain species (Zeug and Winemiller 2007). The timing and frequency of flood events in oxbow lakes of the Brazos River have been demonstrated to enhance the recruitment of predators, such as white crappie (*P. annularis)* and warmouth (*L. gulosus*), and also may influence colonization of lotic-adapted cyprinids (*Cyprinella lutrensis* and *Pimephales vigilax*) that periodically dominate species assemblages of oxbows after flood connection (Zeug et al. 2005).

Evidence for competition organizing perciform assemblages was inferred from trends of morphological similarity within local assemblages that generally was greater than expected with increasing species richness (Tables 4, 5). This pattern is consistent with studies in bird communities (Ricklefs and Travis 1980, Travis and Ricklefs 1983) in which species are added to the periphery of the morphological niche space (expansion) with increasing diversity, while species morphological similarity (NND) remains relatively constant. Given the larger number of coexisting species that consume similar food resources (Werner 1977, Werner and Hall 1977, Jepsen et al. 1997, Montaña and Winemiller 2009), cichlid and centrarchid assemblages are likely to be influenced by competition. If competition is indeed shaping the structure of these assemblages, ecomorphological differences that reflect niche partitioning would be expected (Ricklefs and Miles 1994). In fact, species of *Cichla* and C*renicichla* in the Cinaruco River are gape-limited piscivores that co-occur in many habitats. They also occupy similar regions within morphospace and might be expected to compete. *Cichla* species attain larger sizes and can exploit larger prey than *Crenicichla lugubris* (Montaña and Winemiller 2009, Montaña and Winemiller 2010). Among centrarchids, three species of sunfishes (e.g., *Micropterus salmoides*, *Lepomis macrochirus* and *L. cyanellus*) overlap in diet and food habitat use; however, they differ in morphology and body size (Werner 1977). Body size and shape variation have long been considered to play an important role in niche partitioning (Hutchinson 1959). In this study, body size, body shape, and fin dimension accounted for much of the interspecific morphological variation, suggesting that niche differentiation among co-occurring species in both

cichlid and centrarchid radiations plays an important role in species coexistence (Werner and Hall 1977, Mittelbach 1984, Winemiller et al. 1995). With few exceptions, such as *Lepomis microlophus*, the only molluscivorous species in this study, the two perciform groups have many convergent species with similar body forms associated with congruent patterns of habitat and resource use (see Chapter III).

Given the findings of Winemiller's (1990) latitudinal comparison of freshwater fish assemblages (e.g., low-diversity of Nearctic faunas exhibiting less morphological diversification relative to species-rich tropical faunas), I expected to see greater expansion of morphological volume in relation to increasing species richness in tropical cichlids when compared with temperate centrarchids in similar habitats (Winemiller et al. 1995). Indeed, some ecomorphotypes and specializations of Neotropical cichlids, such as elongate piscivores (*Crenicichla*) and dwarf invertivores (*Apistogramma*), were absent among the centrarchids. The total morphological niche volume occupied by perciforms in each region was greater for tropical cichlids in the Cinaruco River, slightly less in temperate rivers, and by far the least in cichlids from the Tambopata River that had the fewest number of species. If we consider morphological space as a surrogate for niche space, species-rich tropical assemblages are more ecologically diversified (Winemiller 1991) than temperate assemblages.

The main conclusion drawn from my findings is that, during the low-water period, ecological interactions (especially competition) influence patterns of species coexistence in littoral zone habitats of both tropical and temperate floodplain rivers. This conclusion agrees with conclusions from several studies of fish assemblages in littoral zones of

tropical (Rodriguez and Lewis 1997, Willis et al. 2005, Arrington and Winemiller 2006) and temperate (Tonn et al. 1990, Winemiller et al. 2000) lowland rivers. Resource partitioning at the local scale of the mesohabitat could, over time, influence convergent patterns of evolution observed at the interregional scale.

CHAPTER III

ECOMORPHOLOGICAL CONVERGENCE IN NEOTROPICAL CICHLIDS AND NEARCTIC CENTRARCHIDS: EVIDENCE FROM MORPHOLOGY, DIET AND STABLE ISOTOPE ANALYSIS

INTRODUCTION

Ecomorphological convergence is defined as the evolution of similar traits (e.g., physiology, ecology, and morphology) in two or more divergent phylogenetic lineages (Losos 2011). Convergence provides compelling evidence of adaptation in response to environmental factors with relatively predictable effects on trait selection (Schluter 2000). Phenotypic similarity normally results from shared common ancestry, but convergent evolution frequently occurs under environmental conditions that exert selection on functional traits of organisms (Losos 1992, Winemiller et al. 1995, Ruber and Adams 2001, Melville et al. 2006). Thus, if adaptive evolution drives patterns of convergence, organisms with similar niches within similar environmental settings should have common features of functional morphology (Norton and Brainerd 1993, Losos et al. 1998, Stayton 2006, Young et al. 2010).

Studies of convergent evolution have compared morphology and ecology in unrelated organisms inhabiting similar environments (Losos 1992, Winemiller et al. 1995, Huey et al. 2000, Melville et al. 2006, Stayton 2006, Hulsey et al. 2008, Vincent et al. 2009). Given sufficient time, similar selective pressures are predicted to generate convergent phenotypes and ecological performance among distinctly related taxa. For

example, repeated and independent evolution of lizard ecomorphs (*Anolis*) on the Greater Antilles has provided evidence for convergent evolution in response to similar environmental conditions (Losos et al. 1998). Stayton (2006) provided support for convergence in the amount of force produced during jaw closure by herbivororus lizards from divergent lineages. The independent evolution of elongate quadrate bones in natricine snakes supported a model of convergent evolution in feeding performance (i.e., piscivory) between European and North American lineages (Vincent et al. 2009).

Ecomorphological patterns among freshwater fish assemblages have provided strong evidence of convergent evolution (Motta et al. 1995). A recent study of body shapes and trophic morphology (e.g., dentition characters) of eretmodine cichlids in Lake Tanganyika revealed morphological convergence in response to selection for similar dietary niches (Ruber and Adams 2001). Convergence has been observed among fishes possessing highly specialized functional traits (Wainright et al. 2007). The tube-snouted electric fishes from separated orders (gymnotiforms in South America and mormyriforms in Africa), for example, are adapted to grasp and suck immature aquatic insects that burrow or hide in holes in the river substrate (Marrero and Winemiller 1993). Recent studies in the evolution of jaw structure of teleost fishes (Wainright et al. 2004, Hulsey et al. 2008) have demonstrated that divergent phenotypes can subsequently converge into the same area of morphological space (i.e., many-to-one mapping morphology and function, Wainright et al. 2004). In a study of labrid fishes from warm-temperate and tropical reefs, Wainright et al. (2004) and Alfaro et al. (2005) found that different jaw morphologies can produce similar suction force. In their study of

morphological traits in fish assemblages from urbanized streams in tropical and temperate regions, Cunico et al. (2009) found high levels of functional similarity among species from disparate zoogeographic assemblages.

Perciform fishes of the families Cichlidae (cichlids) and Centrarchidae (sunfishes and black basses) are excellent model organisms for research examining evolutionary convergence. These two families evolved independently in different geographic regions, yet, their ecological roles in freshwater communities are very similar (Mittelbach 1984, Layman and Winemiller 2004). In terms of species richness, Neotropical cichlids exceed centrarchids, with approximately 60 cichlid genera and at least 600 species described for South and Central America (López-Fernández et al. 2010). With eight genera and 34 species described, the family Centrarchidae is a relatively young perciform clade endemic to freshwaters of North America (Near et al. 2005). Cichlids and centrarchids both have parental care (Cook and Phillip 2009), occupy similar habitat types (Montaña and Winemiller 2010), and reveal similar patterns of association for functional morphology, feeding mechanics, and diet (e.g., ram- suction feeding modes; Norton and Brained 1993, Galis and Druker 1996). Both lineages contain a variety of trophic groups including benthic invertivores, molluscivores, and piscivores.

Ecomorphology and functional morphology of centrarchids have been extensively studied (Lauder 1982, Winemiller and Taylor 1987, Caroll et al. 2004, Collar et al. 2005, Collar and Wainright 2006), and similar research has been conducted on cichlids (Meyer 1987, Winemiller et al. 1995, Waltzek and Wainright 2003, Hulsey et al. 2008, López-Fernández et al. 2012). Convergence in ecomorphology and ecological

niches of cichlids from three tropical regions (Africa, South and Central America) was demonstrated by Winemiller et al. (1995). In a study examining convergent morphology of molluscivorous and non-molluscivorous heroine cichlids in Central America, Hulsey et al. (2008) found that molluscivory has been gained and lost numerous times in this group, but convergence in durophagy (i.e., ability to eat hard prey) was maintained when comparing molluscivores to closely related species across the Heroini. A recent study by López-Fernández et al. (2012) of the function of the epibranchial lobe in Neotropical geophagines and its relationship with feeding revealed that this pharyngeal structure is correlated with benthic feeding and mouth brooding.

In this study, I examined trophic morphology, stomach contents, and stable isotope ratios in Neotropical cichlid and Neartic centrarchid fishes from four floodplain rivers to investigate ecomorphological convergence. If cichlids and centrarchids reveal one-to-one patterns of morphological and ecological convergence, morphologically similar species are predicted to converge in the same areas of the morphological and dietary space. Consequently, morphologically similar species are expected to occupy similar trophic positions in aquatic food webs. To examine these hypotheses, multivariate ordinations were used to identify patterns of association and overlap among morphological traits and diets between cichlids and centrarchids, and estimates of trophic positions based on stomach contents and isotopic analysis were used to evaluate if morphologically similar species displayed similar trophic positions in food webs.

MATERIALS AND METHODS

Field surveys

Perciform fishes were collected from four lowland rivers: two Neotropical rivers (the Cinaruco in Venezuela and the Tambopata in Peru) and two temperate rivers (the Neches and the Brazos in Texas, USA). These rivers were chosen for comparison to provide similar environmental conditions in terms of geomorphology, sediments, and water quality. The Cinaruco River (study area centered at approximately 6°32´N and 67°24´W) and the Neches (30°35´N and 94°08´W) have clear, slightly-stained, oligotrophic waters, with sandy substrates, low pH, and high transparency. The Tambopata River (study area centered at approximately 12°72´N and 69°28´W) and the Brazos River (30°37´N and 96°37´W) are similar to each other, with neutral pH, high loads of suspended sediments of fine grain size, and high turbidity that limits aquatic primary production.

Cichlids (19 spp. from the Cinaruco, 7 spp. from the lake Tres Chimbadas in the Tambopata) and centrarchids (11 spp. and 10 spp. from the Neches and Brazos, respectively, Table 6) were collected during the low-water period (defined by annual dry season in South America and the summer in North America). In the Cinaruco River, fishes were collected between December of 2005 and May of 2006; in the Tambopata River, collections were made during June and July of 2009, however, only collections from the connected floodplain Lake Tres Chimbadas yielded cichlids. In the Texas rivers, collections were conducted during three summers (May to August) from 2009-2011. Surveys employed multiple sampling gears that varied depending on habitat and

geographic region. In the Cinaruco and Tambopata rivers, open habitats, such as sand banks and leaf litter, in both the river channel and floodplain lakes were sampled with seines, whereas structured habitats containing rocks and submerged wood were sampled with hooks (# 8) baited with small pieces of fish flesh. Collections in the Neches and Brazos rivers included seines in open areas and electrofishing (pulse DC from a handheld boat unit) for habitats containing rocks and submerged wood.

Morphological analysis

Specimens retained for morphological and stomach contents analysis were preserved in 10% formalin and transported to the laboratory. Eleven morphological characters associated with feeding (standard length, body width, head length, gape width, mouth position, snout length, eye diameter, eye position, interorbital distance, gut length, and gill raker length; Gatz 1979, Winemiller 1991) were measured on five adult specimens of each species collected. A vernier caliper (precision = 0.1mm) was used to measure the eleven morphometric distances. The linear morphometric distances were transformed into ratios following the methods by Winemiller (1991). Such transformations remove body size effects and convert linear distances into shape components that have clear functional interpretations.

Table 6. Taxonomic names and tribes for cichlid and centrarchid species surveyed in two tropical and two temperate rivers. Name abbreviations correspond with those in the principal components analysis (PCA). Taxonomic classification for the family Cichlidae follows López-Fernández et al. (2010) and for the family Centrarchidae follows Near et al. (2005).

Cichlidae Species	Tribes	Name abbreviation	Centrarchidae Species	Tribes	Name abbreviation
Cinaruco River			**Neches River**		
Acaronia vultuosa	Cichlasomatini	Avult	*Lepomis cyanellus*	Lepomini	Lcyanel
Aquidens diadema	Cichlasomatini	Adiad	*Lepomis gulosus*	Lepomini	Lgulo
Apistogramma sp.	Geophagini	Asp1	*Lepomis humilis*	Lepomini	Lhumu
Apistogramma hoignei	Geophagini	Ahoig	*Lepomis macrochirus*	Lepomini	Lmacro
Biotodoma wavrini	Geophagini	Bwavri	*Lepomis miniatus*	Lepomini	Lminia
Biotecus dicentrarchus	Geophagini	Bdicen	*Lepomis megalotis*	Lepomini	Lmega
Crenicichla lugubris	Geophagini	Clugub	*Lepomis microlophus*	Lepomini	Lmicro
Crenicichla aff. *wallacii*	Geophagini	Cwall	*Micropterus punctulatus*	Micropterini	Mpunct
Geophagus abalios	Geophagini	Gabal	*Micropterus salmoides*	Micropterini	Msalmo
Geophagus dicrozoster	Geophagini	Gdicro	*Pomoxis annularis*	Archoplitini	Pannul
Heros sp.	Heroini	Heros	*Pomoxis nigromaculatus*	Archoplitini	Pnigro
Hoplarchus psittacus	Heroini	Hpsit	*Centrarchus macropterus*	Centrarchini	Cmacr
Hypselocara coryphaenoides	Heroini	Hcoryp			
Mesonauta insignis	Heroini	Minsig	**Brazos River**		
Satanoperca daemon	Geophagini	Sdaem	*Lepomis cyanellus*	Lepomini	Lcyanel
Satanoperca mapiritensis	Geophagini	Smapi	*Lepomis gulosus*	Lepomini	Lgulo
Cichla intermedia	Cichlini	Cinter	*Lepomis humilis*	Lepomini	Lhumu
Cichla orinocensis	Cichlini	Corino	*Lepomis macrochirus*	Lepomini	Lmacro
Cichla temensis	Cichlini	Cteme	*Lepomis miniatus*	Lepomini	Lminia
			Lepomis megalotis	Lepomini	Lmega
Tambopata River			*Lepomis marginatus*	Lepomini	Lmargi
Aequidens tetramerus	Cichlasomatini	Atetra	*Lepomis microlophus*	Lepomini	Lmicro
Apistogramma luelingi	Geophagini	Alueng	*Micropterus punctulatus*	Micropterini	Mpunct
Apistogramma urteagai	Geophagini	Aurte	*Micropterus salmoides*	Micropterini	Msalmo
Cichlasoma amazonarun	Heroini	Camaz	*Pomoxis annularis*	Archoplitini	Pannul
Crenicichla semicincta	Geophagini	Csemi			
Mesonauta festivus	Heroini	Mfesti			
Satanoperca jurupari	Geophagini	Sjuru			

Dietary analysis

Fishes were dissected and stomachs were removed for analysis of contents. All food items present in the anterior half of the gut were removed and examined under a microscope (Winemiller 1990). Prey items from stomachs were identified to the lowest feasible taxonomic level (e.g., fish to species, invertebrates to order). Individuals with empty stomachs were omitted from analyses. When sufficient specimens were available, at least 30 specimens of each fish species were dissected. Overall, species sample sizes for stomach contents analysis ranged from 13 (rare species, e.g., *Satanoperca mapiritensis*) up > 250 individuals (e.g., *Cichla* and *Crenicichla* species; see Appendix B for samples sizes).

In order to reduce bias from having different specific resources in the two regions, the number of food categories was reduced from approximately 50 taxonomic and functional groups to 24 general categories (Winemiller 1990, Winemiller et al. 1995): Bryozoa, algae, detritus, terrestrial vegetation, sand, microfauna (including water mites, rotifers, worms), mollusks (snails, bivalves), microcrustacea (Cladocera, Ostracoda, Anostraca, Copepoda, Amphipoda), macrocrustacea (shrimp, crayfish), miscellaneous aquatic insects, aquatic insect larvae (Odonata, Trichoptera, Coleoptera, Diptera, Hemiptera, Ephemeroptera, Collembola, Lepidoptera), terrestrial insects (Orthoptera, Hymenoptera, unidentified terrestrial insects), fish, and fish scales. These categories were used for interfaunal comparisons. Volumetric proportions of categories from stomach contents were estimated following the methods of Winemiller (1990).

Tissue samples for stable isotope analysis were taken from three individuals of each species. In addition, samples from shrimp, other aquatic invertebrates, and common primary producers (e.g., benthic algae, seston, C_3 plants, and C_4 plants) were collected from each river. Muscle tissue samples were removed from the dorso-lateral region of fish specimens that had previously been euthanized by immersion in an overdose of anesthesia (tricaine methanesulfonate); for small individuals (<30 mm standard length), the entire specimen (minus the gut) was processed for stable isotope analysis. Samples for stable isotope analysis were preserved in salt following the protocol of Arrington and Winemiller (2002). In the lab, tissues were soaked and rinsed in distilled water to remove the salt, and then dried at 60ºC for 48 h in a drying oven. Dried samples were ground to a fine powder with a mortar and pestle, and then stored in clean glass vials. Subsamples for each ground sampled were weighed and packaged into an Ultra-Pure tin capsule (Costech) and sent to the Analytical Chemistry Laboratory, Institute of Ecology, University of Georgia, for measurement of stable isotope ratios of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$).

Multiple sites, including habitats in the littoral zones of floodplain lakes and the river channel, were sampled in the Cinaruco River. A previous study by Roach et al. (2009) demonstrated low variability in isotopic signatures of conspecific fish from floodplain lakes and the channel of the Cinaruco River. Therefore, we pooled samples from species that occur in both habitat types. In the Tambopata River, all samples were collected from a large floodplain lake (Lake Tres Chimbadas) because surveys conducted in the river channel yielded no cichlids.

Previous studies have shown differences in isotopic values of carbon and nitrogen between river channel and oxbow lakes of the Brazos River (Zeug and Winemiller 2008), therefore samples were taken from both floodplain lakes and the river channel in the Neches and Brazos rivers and analyzed as separate groups.

Data analysis

1. Do cichlids and centrarchids exhibit convergent patterns in morphology? To examine inter-familial patterns of functional morphological traits, ordination of species and local assemblages was conducted using principal components analysis (PCA) on the correlation matrix of log-transformed morphological traits using PC-Ord version 6 (2011).

2. Do cichlids and centrarchids exhibit convergent patterns in their dietary niches? The predominant food items for each species were estimated using volumetric proportions of food items, and subsequently the feeding index (IA_i) proposed by Kawakami and Vazzoler (1980) was calculated. Volumetric proportions of food items also were used to calculate diet similarities for cichlid and centrarchid species within their respective assemblages using Pianka's (1973) symmetrical measure of niche overlap. Values of this index range from near 0 (no overlap) to 1.0 (complete overlap). The analysis of similarity (ANOSIM) test was used to test for significant differences in diets of fish assemblages by river. Using the software PRIMER version 5 (2007), a similarity matrix was generated for the volumetric dietary data using the Bray-Curtis similarity and the observed relationships were compared with random expectations

based on 9,999 permutations. ANOSIM generates a value of R that is scaled to lie between -1 and +1, with a value of zero representing the null hypothesis that there is no diet selection. In addition, a similarity percentage analysis (SIMPER) was conducted to determine which food items were responsible for diet differences among fishes in each river. SIMPER analysis calculates the average dissimilarities between fish species and how much each diet category contributes to average diet dissimilarity (Clarke and Warwick 1994).

Non-metric multidimensional scaling (NMDS) was performed with arc-sine square- root-transformed dietary data to identify primary trophic resources used by cichlid and centrarchid fishes. NMDS was performed using mean proportional volumes of the 24 broad diet categories consumed by species from each river. Subsequently, canonical correspondence analysis (CCA) was performed to examine multivariate relationships between morphological characters and dietary composition. CCA is a multivariate, direct-gradient analysis technique in which a set of species characteristics (in this case, morphology) is related directly to a set of environmental variables (in this case, diet). The technique produces linear combinations (canonical variables) between the two datasets (morphology and diet) with the assumption that the two canonical axes are maximally correlated. The analysis was performed on log-transformed morphological data and arc-sine square-root-transformed dietary data using PC-Ord version 6 (2011).

3. Do cichlids and centrarchids converge in their vertical trophic positions? Trophic positions were calculated based on volumetric stomach contents data and

isotopic data. Individuals with similar diets (based on stomach contents) were expected to have isotopically similar ratios ($\delta^{13}C$ and $\delta^{15}N$) and similar trophic positions, whereas individuals with low diet similarity will be isotopically distant. To test these predictions, bi-plots of $\delta^{13}C$ and $\delta^{15}N$ values of basal sources and consumers were produced to depict patterns of isotopic variation among cichlid and centrarchid species in tropical and temperate rivers and, in the case of temperate rivers, channel and floodplain lake habitats.

Trophic positions of fishes based on stomach contents (TP_{SCA}) were calculated for each river using the formula described in Adams et al. (1983):

$$TP_{SCA} = 1.0 + \Sigma_{j=1}\ TP_j\ (p_j),$$

where TP_j is the trophic position of the prey taxon j and p_{ij} is the fraction of total consumed food (volume) consisting of prey species j. Primary producers were coded as TP = 1, primary consumers feeding only on plant material would have TP =2, carnivores feeding on herbivores would be TP = 3, etc. I defined the trophic positions of the prey items (invertebrates and fishes) by gathering information from published sources containing literature of dietary and stable isotope data for both tropical and temperate freshwater fish assemblages. Vander Zanden et al. (1996) provided estimations of trophic position values for prey items in North American rivers, and Zeug and Winemiller (2008) provided specific information on trophic positions of aquatic consumers in the Brazos River, Texas. Assumptions for estimation of trophic positions of prey items contained in the stomachs of tropical cichlids were based on studies by Jepsen and Winemiller (2002), Layman et al. (2005), and Roach et al. (2009). To

estimate trophic position for piscivorous fishes, including *Cichla* spp., *Crenicichla lugubris*, *Micropterus* spp. and *Pomoxis* spp., fish components in the diets to species of these consumers were identified to genus or family and then assigned trophic position values. Layman et al. (2005) noted that *Cichla* species from Cinaruco River feed predominantly on fishes at trophic position 2 (herbivore and detritivores).

Trophic position from isotopic data (TP_{SIA}) was estimated for each species based on fractionation of $\delta^{15}N$ between consumers and local basal production sources (Vander Zanden and Rasmussen 1999, Post 2002) using the formula:

$$TP_{SIA} = [(\delta^{15}N_{consumer} - \delta^{15}N_{reference})/2.54] + 1,$$

where $\delta^{15}N_{reference}$ was the mean $\delta^{15}N$ of basal sources (C3 plants, seston, and benthic algae), and $2.54^{0}/_{00}$ is the mean trophic fractionation (Vanderklift and Ponsard 2003). Reference values of nitrogen were calculated separately for each river; therefore estimates of trophic positions were directly comparable between the four rivers.

Species trophic positions were calculated separately from stomach contents data (TP_{SCA}) and isotopic data (TP_{SIA} based on $\delta^{15}N$). Trophic position distributions for species assemblages were compared at the river and habitat scales.

For each perciform assemblage, the correlation between TP_{SCA} and TP_{SIA} was evaluated using Pearson's (r), and based on species mean values of TP_{SCA} and TP_{SIA}. I only included species having values for both TP_{SCA} and TP_{SIA}. *A priori*, I tested and confirmed normality of the data. Relationships between trophic position (based on $\delta^{15}N$) and body size (standard length in mm) of each consumer was assessed with the Spearman rank correlation.

To test further the null hypothesis of no significant correlation between phylogeny and morphology and between phylogeny and diet, a Mantel test was performed using the matrices of diet similarity based on stomach contents and morphological similarity based on the matrix of morphological traits. A Partial Mantel test was performed to evaluate the effect of phylogeny (Smouse et al. 1986). The Partial Mantel test estimates the correlation between morphological and dietary matrices while controlling for the effect of the phylogeny. For this study, a matrix of taxonomic distance was constructed by counting the number of nodes that separate each species in the phylogenetic tree (Winemiller et al. 1995; Oliveira et al., 2010). Because I did not have access to branch length data for the most recent phylogeny from molecular data for the Centrarchidae, I used taxonomic levels proxies for relative degrees of evolutionary divergence for both families. Species assigned within the same genus were given a distance of 1, species within the same tribe were given a distance of 2, and species within the same family a distance of 3. Taxonomic classification and relationships were based on the most recent phylogenies for the families Cichlidae (López-Fernández et al. 2010) and Centrarchidae (Near et al. 2005). Mantel and Partial Mantel tests were performed in PC-Ord version 6 (2011).

RESULTS

Morphological patterns

Multivariate ordination of species in morphological trait space revealed high similarity between pairs of species from different lineages (Figure 6). The first two PC axes modeled 51.1% of the variance in morphology of species in the dataset (Table 7). PC1 (29.4% of variance) identified a body-shape gradient contrasting fishes with elongate, streamlined bodies versus fishes having taller and more laterally compressed bodies, the latter group including the majority of sunfishes (Centrarchidae), heroines (Cichlidae) and cichlasomatines (Cichlidae). Positive values on PC1 also were associated with longer gill rakers, larger mouth gape and larger inter-orbital distance, whereas negative values on PC1 were associated with fishes that have a smaller and more terminal mouth and deeper head (Figure 6, Table 7). PC2 (21.7% of variance) contrasted fishes with small body size, such as the dwarf cichlids *Apistogramma* and *Biotoecus*, small terminal mouths, and relatively long guts (large positive scores on PC2) versus those having larger mouths, larger eyes and longer snouts and gill rakers (e.g., in cichlids: *Cichla* spp., *Geophagus* spp., *Satanoperca* spp., *Crenicichla* spp.; and in centrarchids: *Micropterus* spp. and *Pomoxis* spp.; all with large negative scores on PC2) (Figure 6). High morphological overlap occurred between *Cichla* spp. and *Micropterus* spp. due to their relatively streamlined bodies, long gill rakers, large mouths and large eyes.

The first two PC axes separated four distinctive morphological groups. The first group formed by *Cichla, Crenicichla* and *Micropterus* have relatively large heads, large mouths positioned upward, and large eyes. The second group included *Biotodoma wavrini* and species of *Satanoperca*, *Geophagus,* and *Pomoxis*, fishes with relatively short heads, long snouts, and highly protrusible jaws. A third group contained species with short snouts, small mouths, and less jaw protrusibility (e.g., *L. megalotis*, *L. macrochirus*, *L. miniatus* and most cichlasomatines and heroines, Figure 6). The fourth group contained species with relatively large, terminal mouths (*L. cyanellus, L. gulosus L. humilis* and *Acaronia vultuosa*). The sunfish *Lepomis microlophus* did not cluster with any other species, though it displayed morphological traits most similar to the fourth group. This species feeds on mollusks and has hypertrophied pharyngeal jaws that generate strong force to crush shells.

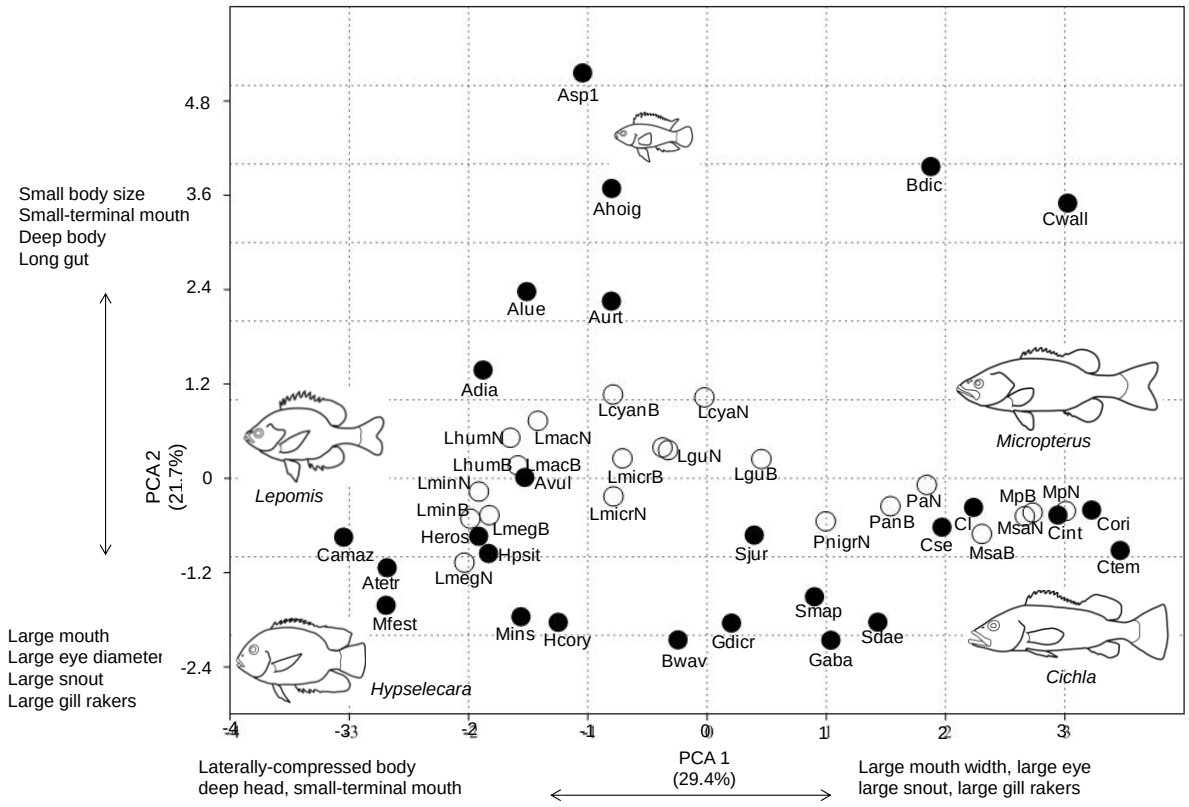

Figure 6. Morphological ordination of perciform fishes from the Cinaruco, Tambopata, Neches and Brazos rivers. Dots represent the average of individual species. Filled dots represent species of the family Cichlidae and open dots represent species of the family Centrarchidae.

Table 7. Principal components analysis (PCA) scores based on 11 functional morphological traits of 26 cichlid and 21 centrarchid species.

	PC1	PC2
Eigenvalues	3.5	2.6
% of variance	29.4	21.7
Morphological traits		
Standard length	0.28	0.46
Head length	-0.22	0.20
Mouth width	-0.34	-0.17
Mouth position	-0.27	0.12
Inter-orbital distance	0.29	-0.33
Gut length	0.21	0.49
Gill length	0.22	-0.3
Eye diameter	0.42	0.18
Eye position	0.07	-0.26
Body depth	0.44	-0.21
Snout length open	0.04	-0.30

Dietary patterns

A total of 4,251 specimens was analyzed for stomach contents (2,140 cichlids from the Cinaruco River, 346 cichlids from the Tambopata floodplain lake, 879 centrarchids from the Neches, and 886 centrarchids from the Brazos, Appendix B). ANOSIM did not reveal significant differences in the diets of cichlids and centrarchids overall ($P < 0.06$; R = 0.14). ANOSIM revealed differences in diets of cichlids from the Cinaruco and centrarchids from both the Neches ($P < 0.01$; R = 0.23) and Brazos rivers ($P < 0.03$; R = 0.19). ANOSIM did not reveal significant differences in diets of cichlids from the Cinaruco River and those from the Tambopata floodplain lake ($P < 0.5$; R = -0.05), nor were significant differences detected between cichlids from the Tambopata

River and centrarchids from the Neches ($P < 0.35$; R = 0.03) and Brazos rivers ($P < 0.62$; R = -0.07).

Overall, the dominant food categories found in diets of both cichlid and centrarchid fishes were benthic macroinvertebrates (e.g., larvae of Odonata, Trichoptera, Coleoptera, Diptera, Ephemeroptera), microcrustacea, macrocrustacea, fish, and fish scales (Appendix B). Mollusks (snails, bivalves, and ostracods) were the main food items identified in the diet of *L. microlophus* in the Neches and Brazos rivers.

NMDS analysis identified two gradients explaining 63.4% of the variance in diet. Axis 1 (43.0% of variance) contrasted consumption of benthic and epibenthic invertebrates versus piscivory (Figure 7). Axis 2 (20.4% of variance) was positively correlated with molluscivory (e.g., *L. microlophus*) and negatively correlated with consumption of other kinds of invertebrates and fish (Figure 7). NMDS clearly grouped a few piscivorous species, the cichlids *Crenicichla lugubris* and *Cichla* spp., and the centrarchids *Micropterus* spp. and *Pomoxis* spp. Large fractions of benthic macroinvertebrates were consumed by substrate-sifting geophagine cichlids. Benthic and epibenthic invertebrates were consumed in large amounts by non-geophagine cichlids (*Cichlasoma*, *Hoplarchus*, *Heros*, *Hypselecara*, *Mesonauta)* and sunfishes (*L. megalotis*, *L. macrochirus*, *L. humilis*, and *L. miniatus*). Generalist species, such as *Acaronia vultuosa, L. gulosus,* and *L. cyanellus,* consumed large amounts of macroinvertebrates, but their diets also contained large fractions of fish and macrocrustacea (Appendix B).

SIMPER analysis identified contributions of individual prey categories to the separation of feeding groups (Figure 7). SIMPER revealed that dietary differences

between the two clear-water river assemblages (Cinaruco cichlids and Neches centrarchids) were due to differential consumption of aquatic insect larvae (39.6%), microinvertebrates (9%), and microcrustacea (7%). Similarly, differences in diets between the Cinaruco cichlids and Brazos centrarchids (turbid-water river assemblage) were associated with differential consumption of aquatic insect larvae (24%) and aquatic microinvertebates (8.3%).

Dietary overlap tended to be high among cichlids within the Cinaruco River (0.40) and Tambopata floodplain lake (0.30), and relatively low among centrarchids within the Neches (0.25) and Brazos (0.13) rivers. Low dietary overlap was observed between geophagine cichlids with laterally compressed bodies (e.g., *Biotodoma*, *Geophagus* spp., *Satanoperca* spp.) and geophagines with elongate bodies (e.g., *Crenicichla*). High inter-faunal dietary overlap was observed between *Cichla* and *Micropterus* (piscivores), *L. cyanellus*, *L. gulosus* and *A. vultuosa* (generalist predators), and among *Cichlasoma*, *Hypselecara*, *Heros*, *Hoplarchus, L. miniatus*, *L. megalotis*, and *L. macrochirus* (aquatic invertebrate consumers, although detritus also was encountered in stomachs; Figure 7).

CCA revealed high correlation between morphology and diet (Table 8). Positive scores on the first morphological axis (CCA1) were associated with small, terminally positioned mouths, short snouts, and short to intermediate length gill rakers (e.g., *Lepomi*s spp. and heroine and cichlasomatine cichlids). This axis was paired with a dietary axis influenced by benthic and epibenthic invertebrate prey and detritus. Negative scores on CCA1 were associated with long gill rakers, large eyes, large mouths

positioned upward, and large bodies, and were paired with a dietary axis influenced by consumption of fish and macrocrustacea. Piscivorous *Cichla* spp., *Micropterus* spp., *Crenicichla lugubris*, and *Pomoxis* spp. had high positive loadings on this pair of axes. Positive scores on the second morphological axis (CCA2) were associated with a long snout and greater jaw protrusion, and were paired with a dietary axis largely influenced by benthic and epibenthic invertebrates. Geophagine cichlids and sunfishes with deep, laterally compressed bodies had high scores on this pair of axes. Negative scores on CCA morphology axis 2 were associated with large eyes, inter-orbital distance, and bodies, and CCA diet axis 2 was associated with consumption of fish and macrocrustacea. The third pair of CCA axes was largely influenced by small terminal mouths and short gill rakers in association with feeding on aquatic invertebrates as well as mollusks. In agreement with CCA results, the Mantel test revealed significant correlations between diet and morphology ($r = 0.29$, $p < 0.0001$). Partial correlations using the Partial Mantel test confirmed relationships between trophic morphology and diet ($r = 0.14$, $p = 0.01$), with no significant effect of phylogenetic distance ($r = 0.12$, $p = 0.06$).

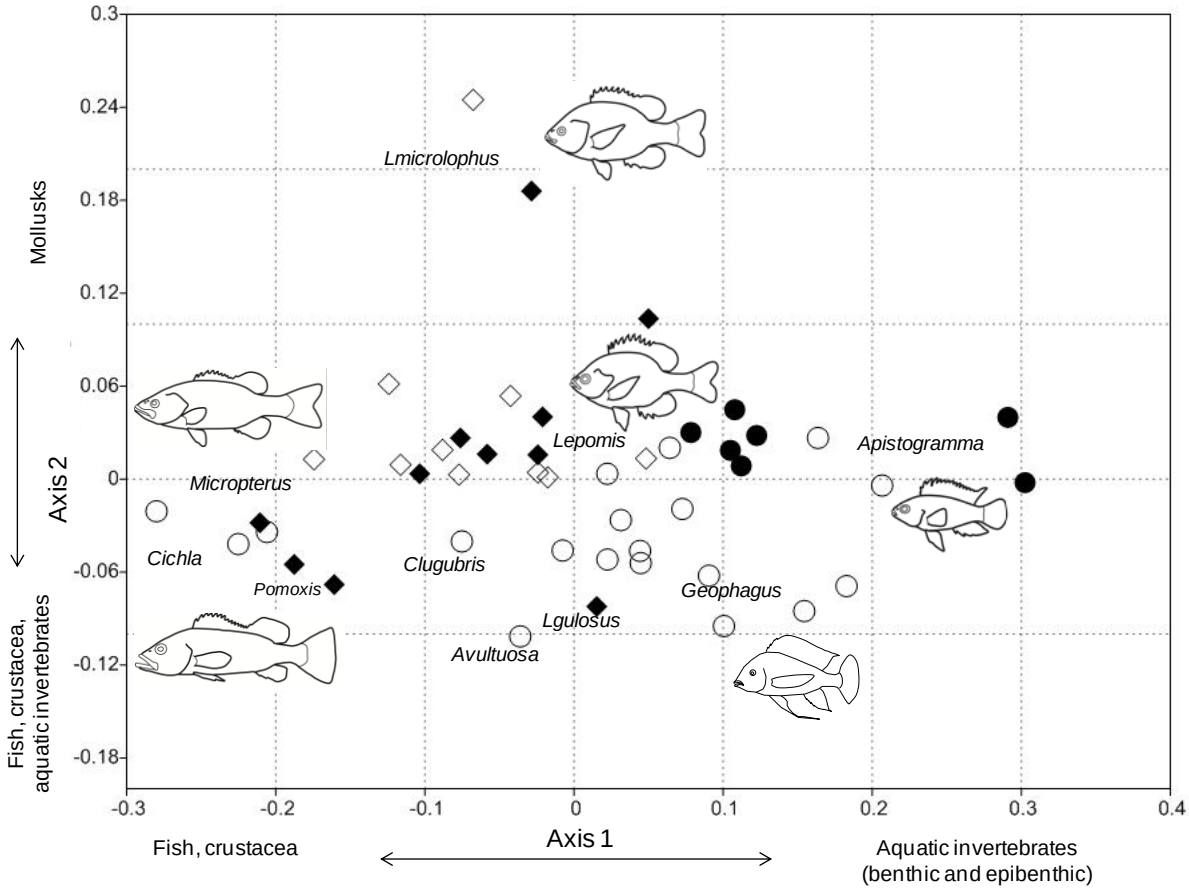

Figure 7. Non-metric multidimensional scaling of dietary data. Each point represents a single species by river observation calculated from the mean volumetric proportions of food categories from stomach contents. Open dots represent cichlid species from the Cinaruco River, filled dots represent cichlid species from Lake Tres Chimbadas in Tambopata, open diamonds represent centrarchid species from the Brazos River, and filled diamonds represent centrarchids species from the Neches River.

Table 8. Statistics associated with the first three axes of the canonical correspondence analysis (CCA) performed on 11 morphological traits and 20 diet categories of cichlids and centrarchids.

	CCA1	CCA2	CCA3
Eigenvalues	0.04	0.01	0.01
% of variance explained	38.40	15.20	5.30
% cumulative explained	38.40	53.60	58.90
Pearson correlation (morphology-diet)	0.86	0.80	0.78
Morphological traits			
Standard length	0.24	-0.46	-0.46
Head length	0.29	-0.05	0.40
Mouth width	1.29	2.94	4.61
Inter-orbital distance	-0.47	-0.30	1.28
Eye position	-0.21	1.33	0.08
Eye diameter	-0.14	-0.61	-0.26
Mouth position	0.31	0.12	0.79
Snout length open	2.64	5.43	-3.40
Gut length	0.33	-0.48	-0.61
Gill raker length	-3.84	1.51	-0.54
Body depth	-0.63	-0.32	-0.07
Food items			
Bryozoa	0.31	0.18	0.11
Diatoms	0.15	0.42	-0.20
Algae	0.33	0.02	0.22
Detritus	0.46	-0.04	0.03
Terrestrial material (leaf litter, seeds, flowers, etc)	0.29	0.34	-0.04
Sand	0.28	-0.13	0.04
Mollusca	0.26	-0.15	0.37
Microfauna	-0.12	0.31	0.26
Microcrustacea	0.19	-0.16	0.27
Crustacea	-0.37	-0.29	-0.25
Odonata	0.20	-0.21	-0.02
Coleoptera	0.28	-0.12	0.17
Diptera	0.22	0.04	0.32
Ephemeroptera	-0.11	0.29	-0.03
Trichoptera	0.21	0.22	0.16
Terrestrial insects	-0.18	-0.03	-0.27
Fishes	-0.39	-0.22	-0.33
Scales	0.45	0.17	-0.37

Isotopic patterns

Cichlid assemblages from Neotropical rivers had greater $\delta^{13}C$ ranges than temperate centrarchid assemblages (Figure 8a-b). For example, $\delta^{13}C$ for cichlids from the Cinaruco River ranged from -25$^{0}/_{00}$ to -35$^{0}/_{00}$, and $\delta^{13}C$ varied between -29$^{0}/_{00}$ to -36$^{0}/_{00}$ for cichlids from the Tambopata floodplain lake (Figure 8a-b). For centrarchids in the Neches River, $\delta^{13}C$ ranged from -25.5$^{0}/_{00}$ to -29$^{0}/_{00}$, and between -22$^{0}/_{00}$ to approximately -28$^{0}/_{00}$ for those in the Brazos River (Figure 8c-d).

Piscivores in both cichlid (e.g., *Cichla* spp. and *Crenicichla lugubris)* and centrarchid (e.g., *Micropterus* spp. and *Pomoxis* spp.) assemblages had highest $\delta^{15}N$ values (Figure 8a-c-d). Sunfishes, cichlasomatines, heroines and most geophagines, all of which are known to consume large amounts of aquatic invertebrates, had intermediate to low $\delta^{15}N$ values (approximately between 6-8.5$^{0}/_{00}$ for cichlids in the Cinaruco, 6.9-8.3$^{0}/_{00}$ for cichlids in the Tambopata floodplain lake, and between 8-12$^{0}/_{00}$ for sunfishes in the Neches and Brazos rivers). The cichlasomatine cichlid, *Acaronia vultuosa*, and the sunfishes *L. gulosus* and *L. cyanellus,* which consume both aquatic invertebrates and fishes, had intermediate $\delta^{15}N$ values ranging from approximately 8.0$^{0}/_{00}$ for *A. vultuosa*, 9.1$^{0}/_{00}$ and 10.0$^{0}/_{00}$ for *L. gulosus* in the Neches and Brazos rivers, and 10.1$^{0}/_{00}$ to 12.8$^{0}/_{00}$ for *L. cyanellus* in the Neches and Brazos rivers, respectively. $\delta^{15}N$ signatures among species assemblages from different rivers varied significantly ($F = 42.1$, $p < 0.001$). Nitrogen isotope values of consumers from the Neches and Brazos rivers were significantly different (student's *t*-test, $t = 2.29$, $p = 0.03$), with Brazos fish having higher values (Figure 8d).

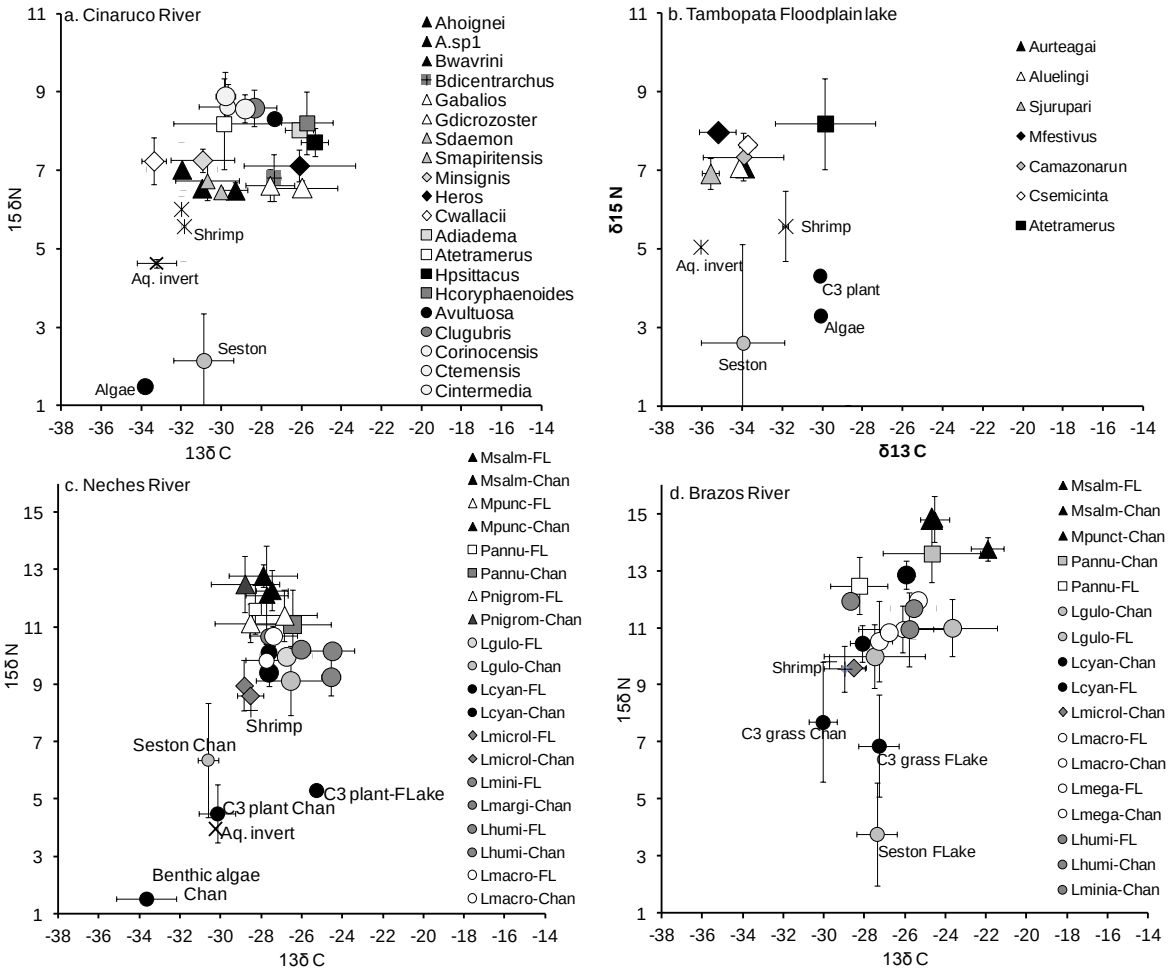

Figure 8. Bi-plot of $\delta^{13}C$ and $\delta^{15}N$ of cichlid and centrarchid species, invertebrates and basal carbon sources. Values represent means and ± standard deviations. a) clear-water Cinaruco River, b) clear-water floodplain Lake Tres Chimbadas in Tambopata River, c) clear-water Neches River, d) turbid-water Brazos River. Samples for the Neches and Brazos rivers were taken from the floodplain lake (FL) and river channel (Chan).

Comparison of vertical trophic structure based on stomach contents analysis and stable isotope analysis

Overall, trophic positions estimated by the two methods stomach contents data (TP_{SCA}) and isotopic data (TP_{SIA}) were strongly correlated both for cichlids and centrarchids (Figure 9) (r^2 for cichlid data = 0.74, $p < 0.0001$; r^2 for centrarchid data = 0.77, $p < 0.0001$). The molluscivorous centrarchid *Lepomis microlophus* which occurs in both the Neches and Brazos rivers, was an outlier and had the lowest trophic position (Figure 9).

Estimates of trophic positions based on TP_{SCA} and TP_{SIA} revealed a pattern in which invertivorous and generalist cichlids had lower trophic positions calculated from stomach contents analysis compared to estimates from stable isotope data (Figure 10a). For centrarchids, several invertivores also had lower trophic positions calculated from stomach contents data compared to estimates from stable isotope data (Figure 10b). The two methods yield fairly concordant estimates for piscivorous cichlids and centrarchids, placing these species at high trophic levels (Figure 10a-b).

According to the dietary method, piscivorous cichlids and centrarchids had the highest trophic positions. TP_{SCA} of *Cichla* spp. varied between 4.3–4.6, whereas in *Micropterus* spp. TP_{SCA} was 3.5–4.5 (Figure 10a-b). Most invertivorous and generalist cichlids had TP_{SCA} values between 1.1–2.1 (invertivores, e.g., *Apistogramma* spp. *Aequidens diadema*, *Geophagus* spp.) to 3.2 (generalists, e.g., *Hypselecara coryphaenoides*) (Figure 9a). Invertivorous centrarchids in the Neches and Brazos rivers had $TPsc_A$ between 1.97–2.5 (e.g., *L. miniatus*, *L. humilis*, *L. megalotis*), whereas

generalists such as *L. cyanellus*, *L. gulosus* and *L. macrochirus* had TP_{SCA} between 2.77–3.02. In the Tambopata floodplain lake, the cichlid assemblage consisted primarily of invertivores ($TP_{SCA} < 2.0$) with one generalist species *Crenicichla semicincta* with $TP_{SCA} = 2.2$. Based on TP_{SCA}, *L. microlophus* had the lowest trophic position of any centrarchid in the both Neches (1.93) and Brazos (1.75) rivers.

Trophic position based on analysis of nitrogen isotope ratios (TP_{SIA}) showed continuous gradients for cichlid and centrarchid assemblages (Figure 10a-b). TP_{SIA} of cichlids ranged from 2.7 (invertivores, e.g., *S. jurupari*) up to 4.1 (piscivores, e.g., *Cichla* spp.) (Figure 10a). Among centrarchids, *Lepomis microlophus* had the lowest TP_{SIA} estimated (~ 1.8). Other centrarchid species followed trends similar to cichlids, with TP_{SIA} ranging from 2.8 for invertivorous to 4.3 for piscivores (Figure 10b). Centrarchids from the river channel had significantly different TP_{SIA} than those in floodplain lakes of the Neches River ($t = 2.36$, $p = 0.02$), but no statistically significant differences were detected among species from the river channel and floodplain lakes of the Brazos River ($t = 0.16$, $p = 0.87$).

A relationship between trophic position and body size was observed for cichlids in the Cinaruco ($r_s = 0.51$, $p = 0.02$) and centrarchids in the Neches ($r_s = 0.68$, $p = 0.02$) and Brazos rivers ($r_s = 0.70$, $p = 0.02$), but no correlation was observed for cichlids of the Tambopata lake ($r_s = 0.03$, $p = 0.90$) where large-bodied cichlids were absent. Large-bodied piscivores, including *Cichla* spp., *C. lugubris, Micropterus* spp. and *Pomoxis* spp., had high trophic positions, whereas medium-and-small-bodied trophic generalists and invertivores had intermediate to low positions, respectively (refer to Appendix B for ranges of standard length ranges of species examined). Overall, perciform species with similar morphology tended to have similar trophic positions. Exceptions were the centrarchids *Pomoxis* spp. and the geophagine cichlids with laterally compressed bodies that occupied similar areas within multivariate morphospace, but revealed large dietary differences that were reflected in different trophic position estimates; *Pomoxis* spp. had higher trophic position along with other piscivores, whereas invertivorous geophagine cichlids had lower trophic positions.

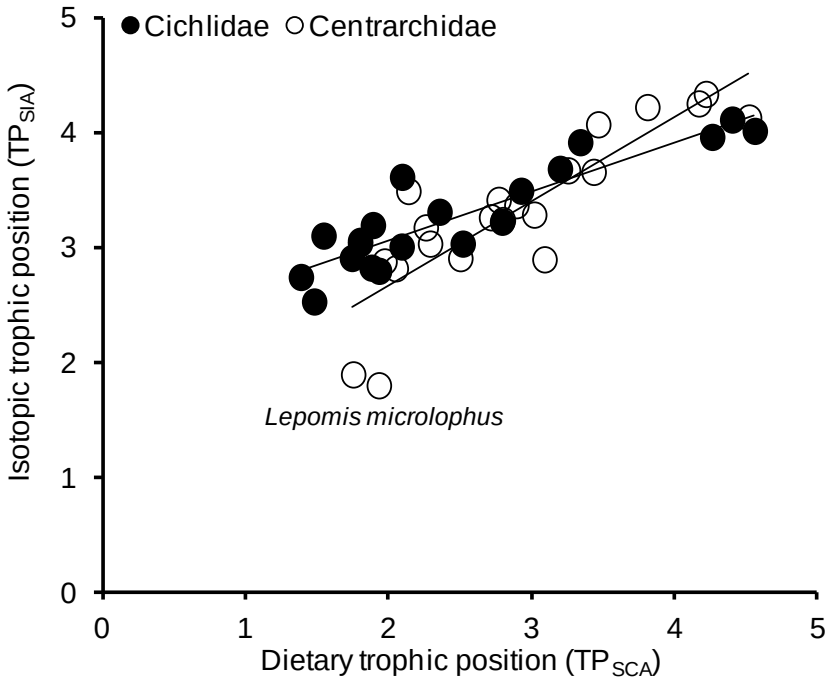

Figure 9. Comparison of trophic position values for cichlid and centrarchid assemblages derived from TP_{SCA} (volumetric dietary data) vs. TP_{SIA} ($\delta^{15}N$). r^2 for the cichlid dataset = 0.74, $p < 0.0001$; r^2 for the centrarchid dataset = 0.77, $p < 0.0001$.

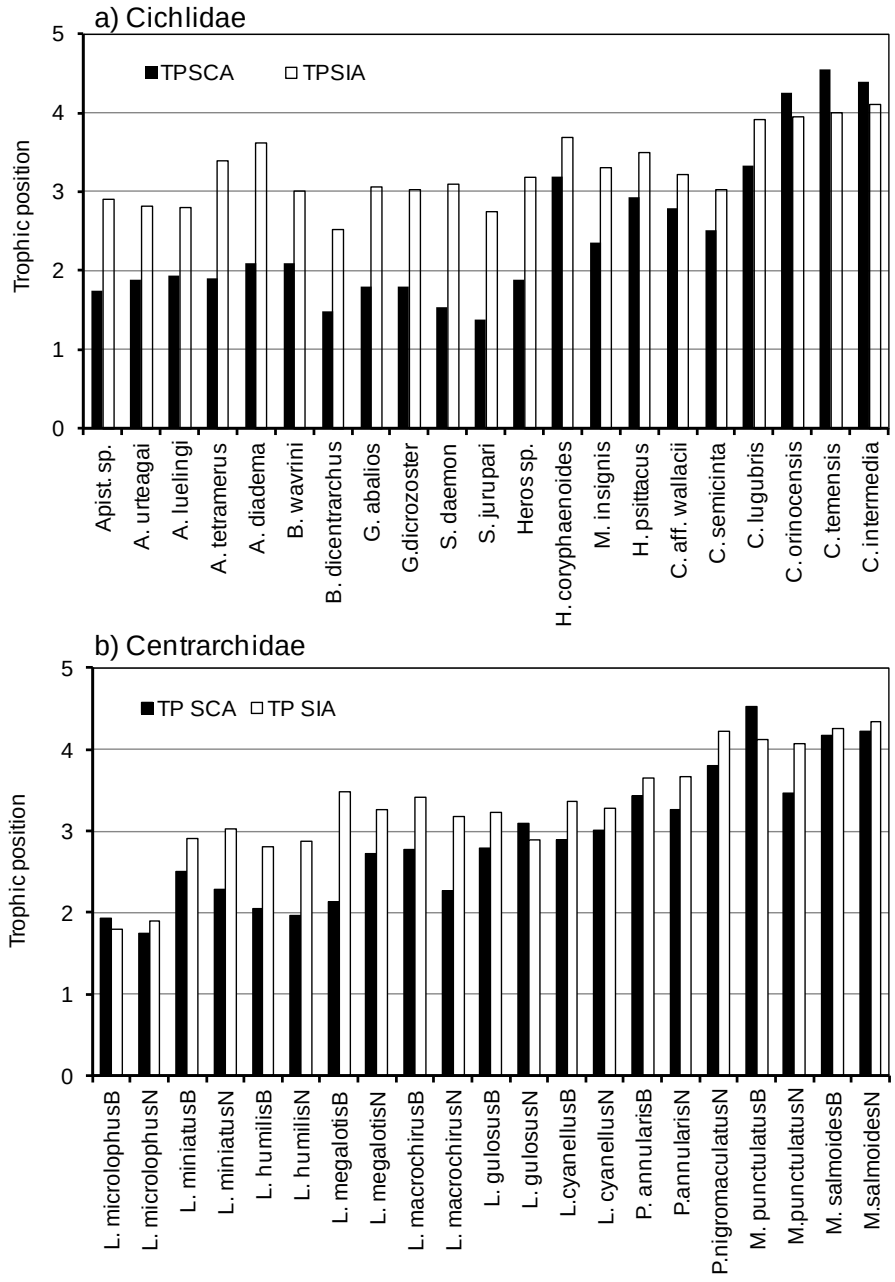

Figure 10. Comparison of trophic position values for a) cichlid and b) centrarchid assemblages derived from TP_{SCA} (volumetric dietary data) vs. TP_{SIA} ($\delta^{15}N$).

DISCUSSION

Despite the fact that there are more species of Neotropical cichlids and that their lineage is older than that of Nearctic centrarchids, the ecomorphological patterns observed in perciform assemblages from lowland streams represent a convergent evolutionary response to similar ecological challenges. Several species of cichlids and centrarchids have independently evolved to occupy lentic habitats and backwaters in river channels and floodplain lakes, as well as flowing waters in the river channel, often in association with structurally complex habitats. Likewise, these two distantly related lineages reveal similar distributions of functional traits that allow various species in both groups to exploit similar kinds of food resources, including aquatic insects, crustacea, mollusks, and fish.

Several studies have demonstrated ecomorphological convergence across freshwater percomorph fishes (Winemiller et al. 1995, Ruber and Adam 2001, Knouft 2003, Hulsey et al. 2008, Carlson and Wainright 2010). Similarities in body and jaw shapes between several species of cichlids and centrarchids imply that these characters are adaptive for specific forms of habitat use and/or exploitation of prey of various types (Westneat and Wainright 1989, Liem 1991, Norton and Brainerd 1993, Wainright et al. 2001). Although my study is correlative, ecomorphological axes derived from PCA and CCA have obvious functional interpretations derived from biomechanical studies in cichlids (Wainright et al. 2001) and centrarchids (Caroll et al. 2004). *Cichla* and *Micropterus* species have streamlined bodies for rapid acceleration and large protrusible mouths for high attack velocity and capture of elusive prey (Norton and Brainerd 1993).

Micropterus salmoides is phylogenetically more distant from *P. nigromaculatus* than *L. macrochirus* (Near et al. 2005), but in terms of functional morphology and diets, *M. salmoides* is much more similar to the former (Caroll et al. 2004). The basal Neotropical cichlid genus *Cichla* and the geophagine genus *Crenicichla* present a similar case of intrafamilial convergence. In multivariate morphospace, the cichlids *Cichla* and *Crenicichla* and the centrarchids *Micropterus* and *Pomoxis* occupied a region that coincides with the ram-feeding models described by Wainright et al. (2001). Ram feeders have large mouths with greater jaw protrusion that helps to increase velocity during prey attack (Waltzek and Wainright 2003) and that increases the distance from which prey can be drawn into the mouth via suction (Wainright et al. 2001). In combination, these trophic morphological characters are thought to increase the efficiency for feeding on elusive prey. Based on dietary and isotopic data, I observed strong association between diets and trophic positions of piscivorous *Cichla* and *Micropterus* species. Both of these psicivorous genera occupied high positions in their respective food webs. *Pomoxis* spp. and *C. lugubris* were not strongly convergent in morphology, but these fishes nonetheless occupied similar positions in dietary and isotopic space, with fishes and macrocrustacea dominant in diets.

Heroine and cichlasomatine cichlids and sunfishes (*Lepomis*) were morphologically convergent, and both groups feed on small prey probably using suction and biting modes (Barel 1983, Liem 1993, Norton and Brainerd 1993). The relatively small mouths and compacted jaws possessed by some of these fishes can produce powerful bites but with less suction (Barel 1983, Norton 1995). These fishes also possess

pointed conical oral teeth that should enhance their ability to grasp prey. Most sunfishes, heroines and cichlasomatines contained large fractions of benthic and epibenthic invertebrates in their gut contents, and this is consistent with their intermediate to low estimates for trophic position (Figure 8). My findings contradict previous studies in which several of the species of heroines and cichlasomatines examined here were described as detritivores (Lasso and Machado 2000). I found that their diets were dominated by benthic and epibenthic invertebrates. Among sunfishes, *Lepomis gulosus* and *L. cyanellus* shared an ecomorphological space with the heroine cichlid *Acaronia vultuosa*. Dietary and isotopic estimates placed these three species together as generalist-predators that feed on diverse prey.

Differences in the trophic positions of several species based on the two methods suggest that it is likely that the isotopic method more accurately estimated the number of trophic transfers than did the dietary method. Error in diet-based trophic position calculations could arise from *a priori* assignment of trophic levels for prey taxa. A potential source of bias for trophic position calculations based on stable isotope analysis could be the low number of samples used, which did not cover the range of size classes used for stomach contents analysis. In addition, there could be error in assigning the constant for trophic fractionation of $\delta^{15}N$ (Post 2002).

The cichlids *Geophagus* spp. and *Satanoperca* spp. and the centrarchids *Pomoxis* spp. have highly protrusible jaws that help to generate suction (Norton and Brainerd 1993, Wainright et al. 2001, Caroll et al. 2004) and laterally compressed bodies that are associated with efficient lateral maneuverability (Caroll et al. 2004). Suction feeding in

percomorphs involves a rapid buccal expansion and generation of negative pressure in the orobranchial chamber followed by jaw protrusion and opening that generates water current that draws prey into the mouth. Protrusion of the premaxilla accompanied the evolution of winnowing behavior (orobranchial chamber sifting of substrate and food particles) in cichlids (Hulsey and Garcia de León 2005, López-Fernández et al. 2012), surf perches (Drucker and Jensen 1991), and carps (Sibbing et al. 1986). In substrate-sifting geophagine cichlids, the subterminal mouth position seems to be an important feature facilitating benthic feeding (López-Fernández et al. 2012). Jaw protrusion is important not only for ram feeders (e.g., *Cichla* spp. and *Micropterus* spp.), zooplanktivores, and epibenthic gleaners that use suction (e.g., *L. macrochirus*, *Heros*), but also for benthivorous substrate sifters (e.g., *Geophagus* and *Satanoperca* species) (Wainright et al. 2001). Substrate-sifting geophagines had relatively low trophic positions that reflected consumption of large fractions of aquatic invertebrates, such as chironomid, trichopteran and ephemeropteran larvae.

Specialized molluscivory was only observed for *Lepomis microlophus* in the Neches and the Brazos rivers. The fusion of the pharyngeal jaw and large rounded molariform teeth in this species are associated with enhanced ability to crush hard-bodied prey (Lauder 1983). The ability of *L. microlophus* to feed on hard-shelled organism provides access to food resources less effectively used by other sunfishes. The two Neotropical cichlid assemblages did not have any molluscivores because snails and mussels were absent from these two rivers, probably due to the extremely low hardness of the water. Nevertheless, molluscivory has been reported for the Central American

heroine cichlids in the genera *Herichthys* (Hulsey et al. 2008) and *Astatheros* (Winemiller et al. 1995) and the South American cichlasomatine genus *Aequidens* (Winemiller et al. 1995).

Interspecific variation in diet within fish assemblages has been attributed to mouth size (Wainright and Richard 1995) and body size (Keast and Webb 1966, Gatz 1979). Within the perciform families investigated here, piscivory was correlated with fishes having large bodies as well as large mouth gapes. Similar patterns have been observed in other studies dealing with tropical cichlids (Winemiller et al. 1995, Jepsen et al. 1997, Montaña et al. 2011) and temperate centrarchids (Keast and Webb 1966, Hambright 1991) as well as in other teleost fishes (Hugueny and Pouilly 1999). The evolution of feeding relationships in fishes was discussed by Liem (1991), who emphasized the importance of feeding modes (ram feeding and suction feeding) in predators. Norton and Brainerd (1993) attributed convergence in feeding modes of *Cichla ocellaris* (Cichlidae) and *Micropterus salmoides* (Centrarchidae) to selection for powerful suction during prey attack. I predicted that morphologically similar species would have similar feeding habits and occupy similar trophic positions; in fact, this hypothesis was supported for piscivores as well as several invertivores.

Kerr and James (1975) proposed that if environmental conditions impose constraints on adaptation, and these constraints are simultaneously expressed in morphology and ecology, then predictions can be made as to which morphological attributes are associated with a specific ecological niche and *vice versa*. In fishes, a striking case is presented by the electric gymnotiform and mormyriform fishes. Despite

arising from very distantly related ancestors and occupying different geographic regions, these fishes are phenotypically and ecologically similar in many important respects (Fink and Fink 1981), including body form, swimming behavior, feeding behavior, reproductive behavior, nocturnal activity, and generation and reception of electric impulses (Marrero and Winemiller 1993, Winemiller and Adite 1997, Sullivan et al. 2000, Lovejoy et al. 2010). Marrero and Winemiller (1993) examined morphological and apparent ecological convergence in two tube-snouted gymnotiform and mormyriform fishes. They found that the two species have independently evolved specialized head morphologies to extract benthic invertebrates that burrow and refuge in tiny holes in clay substrate and woody debris. Independent evolution of phenotypic and ecological specializations in these two electric fish groups is obvious, which results from selection for feeding on a specific food resource in specific microhabitats. In the case of cichlids and centrarchids, these fishes occupy similar niche spectra, supporting the hypothesis of convergent adaptive evolution (Schluter 2000). Relationships between morphology and diets were independent of the phylogenetic (taxonomic) distances, further indicating morphological convergence between these two perciform lineages.

My results are concordant with other studies showing strong relationship between morphology and diet in fish assemblages (Gatz 1979, Winemiller et al. 1995, Hugueny and Pouilly 1999, López-Fernández et al. 2012) and refute the proposition put forth by Douglas and Matthews (1992) that valid ecomorphological studies are restricted to fishes within same family. Although my study revealed ecomorphological convergence between these distantly related lineages, greater precision could be

achieved by adopting methods such as direct measurements of selection (Losos 2011) and more detailed comparative analysis based on recent phylogenies that include branch lengths instead of categorical hierarchy based on taxonomy. A key (and undoubtedly wrong) assumption for the use of taxonomic divisions is that rates of evolutionary change are uniform for all branches between a given taxonomic level and the adjacent level. Previous biomechanical studies have demonstrated convergence in feeding mechanisms (Norton and Brainerd 1993) between tropical cichlids and temperate centrarchids. However, my study is the first one that attempts to quantify morphological and ecological similarities of coexisting perciform from natural habitats in lowland rivers.

CHAPTER IV

CONCLUSIONS

General Conclusions

Evolutionary ecologists study morphological traits to infer aspects of functional and community ecology. Morphological traits reflect the way in which organisms physically interact with their environments, but also facilitate or constrain an organism's ability to perform certain functions (Wainright 1994). In the study presented here, I used morphological characteristics and feeding ecology of two independent perciform lineages, Neotropical cichlids and Nearctic centrarchids, to demonstrate the extent that species in these two lineages display evolutionary convergence. Similarly, morphological diversity of species in these two families was compared in local assemblages to investigate patterns of species richness in relation to different habitat types and infer ecological processes allowing species coexistence.

In Chapter II, I reported findings from multivariate statistical analysis that examined interfaunal patterns of species richness in four floodplain rivers using two spatial scales: macrohabitats (e.g., channel versus lagoon) and mesohabitats (local patch). I used the distribution of species in assemblage morphospace to infer niche relationships and potential mechanisms of species coexistence (Winemiller 1991, Ricklefs and Miles 1994, Silva et al. 2010). Results revealed that morphology explained a significant part of the interfaunal patterns of species similarity in form and function. Results from null models suggest nonrandom distribution of local perciform

assemblages within morphological niche space. In both perciform assemblages, species appeared to be more separated within the local assemblage niche space than predicted at random. Changes in average morphological similarity (measured by mean NND) among species when increasing the number of species was inferred as evidence for competitive interactions organizing local perciform assemblages, with most cases supporting the niche expansion model in these mesohabitats of tropical and temperate floodplain rivers. Neotropical cichlids and temperate centrarchids contain a large number of species that often may overlap in their use of resources (e.g., food and habitat use). However, biotic interactions within these local assemblages may result in species moving to the periphery of the morphological niche space (niche expansion), when more species are added to the assemblages, consequently partitioning resources at a finer level that allows local coexistence. For cichlid assemblages in the Cinaruco River, morphological niche space was greater than expected by chance as species richness increased. This finding is not surprising for assemblages in species-rich tropical rivers, in which species interaction and habitat structural complexity maintain high species richness (Winemiller 1990).

Overall, randomization analyses pointed toward competition organizing local perciform assemblages. However, trends in the evenness of species packing within morphological niche space in relation to species richness were inconsistent among the twenty mesohabitat assemblages from tropical and temperate rivers. Structurally complex mesohabitats (e.g., leaf litter, wood, rock shoal) tended to have greater

evenness, which suggests that species interactions may play a greater role in determining assemblage structure in these habitats compared to less complex habitats.

In Chapter III, I analyzed morphological traits associated with feeding, diet data, and isotope ($\delta^{13}C$ and $\delta^{15}N$) data to investigate whether Neotropical cichlids are morphologically and ecologically convergent with temperate centrarchids. Results indicated that cichlids and centrarchids have evolved similar morphological adaptations associated with habitat and food resource use. Combining morphology and dietary analyses, I demonstrated that several species of cichlids and centrarchids are morphologically and ecologically convergent. Both assemblages showed the same set of ecomorph types that occupy similar trophic niches, for example benthic and epibenthic invertivores, trophic generalists, and piscivores. The substrate-sifting invertivore niche was only present in the cichlid assemblages, whereas molluscivores were only observed in the two temperate centrarchids assemblages. Fishes in both perciform lineages occupied regions of morphospace that coincide with the ram and suction feeding modes described by Wainright et al. (2001). Ram feedering piscivores had larger mouths and greater jaw protrusion, whereas many of the benthivorous-invertivores had smaller, more compact jaws that produce less suction but more powerful bites for removing organisms attached to the substrate. Although in most respects this study found ecomorphological patterns consistent with previous studies of centrarchids, I believe that future research involving comparative biomechanical analysis in species-rich lineages will provide a fruitful area for understanding adaptation in perciform radiations. Ecomorphological convergence provides strong evidence for adaptation involving form and function

constraints. Research in this area should continue to strive for a better understanding of evolutionary forces driving species adaptation to specific environmental conditions. The use of phylogenetic distance (e.g., branch length) instead of taxonomic distance (used in this study) should provide more precise estimates of the phylogenetic constraints and convergence.

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APPENDIX A

Appendix A. Simple linear regressions (r, p-values), coefficient of determination R^2 (for observed and random data), slope values (for observed and random data) and p-values resulted from t-test analysis between observed and random analysis in the regression slopes of the three measures of morphological (MNND, SDNND, CD) dispersion of cichlids and centrarchids in relation to species richness. Asterisk (*) in the linear regression column represents significant relationships between the morphological distance index and the number of species.

River	Macrohabitat	Mesohabitat	Dependent variable	Linear regression (r, p-values)	R_{obs}^2	$Slope_{obs}$ (y)	R_{random}^2	$Slope_{random}$ (y)	slope reg. (p-values) (Observed vs Random)
Cinaruco	Floodplain lake	Wood	Mean NND	0.04, 0.84	0.001	-0.01	0.94	-0.03	t: 0.33, p = 0.19
	Floodplain lake	Leaf litter	Mean NND	0.44, 0.05*	0.2	-0.01	0.92	-0.003	t: 2.75, p = 0.09
	Floodplain lake	Rocks	Mean NND	0.84, 0.001*	0.7	-0.04	0.94	-0.03	t: 0.63, p = 0.53
	Floodplain lake	Sand bank	Mean NND	0.16, 0.39	0.02	-0.01	0.86	-0.01	t: 1.07, p = 0.62
	Channel	Wood	Mean NND	0.43, 0.05	0.31	-0.03	0.96	-0.02	t: 2.01, p = 51
	Channel	Leaf litter	Mean NND	0.54, 0.89	0.21	-0.02	0.98	-0.02	t: 0.1, p = 0.99
	Channel	Rocks	Mean NND	0.45, 0.03	0.21	-0.04	0.93	-0.01	t: 0.94, p = 0.05
	Channel	Sand bank	Mean NND	0.53, 0.37	0.06	-0.01	0.94	-0.01	t: 0.92, p = 0.06
Neches	Floodplain lake	Wood	Mean NND	0.16, 0.56	0.03	0.003	0.96	-0.01	t: 3.9, p = 0.01
	Floodplain lake	Leaf litter	Mean NND	0.21, 0.39	0.05	-0.01	0.98	-0.01	t: 4.8, p = 0.01
	Channel	Wood	Mean NND	0.43, 0.03*	0.2	-0.03	0.94	-0.01	t: 1.09, p = 0.08
	Channel	Rocks	Mean NND	0.66.0.03*	0.43	-0.04	0.97	-0.01	t: 0.7, p = 0.49
	Channel	Sand bank	Mean NND	0.34, 0.11	0.12	-0.04	0.92	-0.01	t: 0.47, p = 0.63
Brazos	Floodplain lake	Wood	Mean NND	0.17, 0.49	0.03	0.01	0.93	0.002	t: 4.51, p 0.02
	Floodplain lake	Leaf litter	Mean NND	0.19, 0.36	0.04	-0.01	0.95	-0.02	t: 2.49, p =0.21
	Channel	Wood	Mean NND	0.31, 0.14	0.09	-0.02	0.9	0.01	t: 6.2, p = 0.01
	Channel	Rocks	Mean NND	0.43, 0.14	0.19	-0.03	0.93	0.003	t: 5.03, p = 0.04
	Channel	Sand bank	Mean NND	0.19, 0.39	0.04	-0.01	0.93	-0.01	t: 3.26, p = 0.01
Tambopata	Floodplain lake	Wood	Mean NND	0.24, 0.40	0.01	0.02	0.98	-0.03	t: 1.38, p = 0.14
	Floodplain lake	Leaf litter	Mean NND	0.18, 0.54	0.03	0.02	0.97	-0.03	t: 3.2, p =0.05

Appendix A. Continued

River	Macrohabitat	Mesohabitat	Dependent variable	Linear regression (r, p-values)	R_{obs}^2	$Slope_{obs}$ (y)	R_{random}^2	$Slope_{random}$ (y)	Slope reg. (p-values) (Observed vs Random)
Cinaruco	Floodplain lake	Wood	SD NND	0.32, 0.23	0.11	-0.01	0.97	-0.01	t: 0.47, p = 0.63
	Floodplain lake	Leaf litter	SD NND	0.04, 0.87	0.001	0.001	0.99	-0.01	t: 1.47, p = 0.15
	Floodplain lake	Rocks	SD NND	0.76, 0.003*	0.57	-0.02	0.99	-0.01	t: 0.29, p = 0.80
	Floodplain lake	Sand bank	SD NND	0.17, 0.37	0.02	-0.02	0.99	-0.01	t: 1.64, p = 0.66
	Channel	Wood	SD NND	0.11, 0.62	0.01	-0.01	0.96	-0.01	t: 1.42, p = 0.16
	Channel	Leaf litter	SD NND	0.14, 0.62	0.02	0.003	0.99	-0.01	t: 4.5, p = 0.001
	Channel	Rocks	SD NND	0.04, 0.87	0.42	-0.02	0.99	-0.01	t: 0.08, p = 93
	Channel	Sand bank	SD NND	0.20, 0.59	0.02	0.003	0.99	-0.01	t: 4.34, p = 0.01
Neches	Floodplain lake	Wood	SD NND	0.06, 0.81	0.001	-0.001	0.95	-0.001	t: 5.3, p = 0.04
	Floodplain lake	Leaf litter	SD NND	0.04, 0.87	0.002	0.001	0.98	-0.003	t: 5.05, p = 0.01
	Channel	Rocks	SD NND	0.61, 0.06	0.37	-0.03	0.97	-0.001	t: 0.74, p = 0.46
	Channel	Wood	SD NND	0.49, 0.02*	0.16	-0.02	0.98	-0.002	t: 2.3, p = 0.03
	Channel	Sand bank	SD NND	0.21, 0.92	0.12	-0.02	0.84	-0.001	t: 6.93, p= 0.05
Brazos	Floodplain lake	Wood	SD NND	0.32 0.18	0.1	0.01	0.96	0.01	t: 2.4, p = 0.3
	Floodplain lake	Leaf litter	SD NND	0.21, 0.21	0.07	0.01	0.98	-0.01	t: 5.04, p = 0.01
	Channel	Rocks	SD NND	0.25, 0.40	0.03	-0.01	0.98	0.01	t: 4.4, p = 0.02
	Channel	Wood	SD NND	0.25, 0.23	0.01	-0.004	0.96	0.001	t: 6.68, p = 0.01
	Channel	Sand bank	SD NND	0.41, 0.06	0.16	-0.02	0.98	-0.01	t: 7.2, p = 0.01
Tambopata	Floodplain lake	Wood	SD NND	0.40, 0.12	0.16	-0.03	0.82	-0.01	t: 4.47, p = 0.02
	Floodplain lake	Leaf litter	SD NND	0.17, 0.54	0.07	0.01	0.99	-0.01	t: 4.2, p = 0.01

Appendix A. Continued

River	Macrohabitat	Mesohabitat	Dependent variable	Linear regression (r, p-values)	R_{obs}^2	$Slope_{obs}$ (y)	R_{random}^2	$Slope_{random}$ (y)	Slope reg. (p-values) (Observed vs Random)
Cinaruco	Floodplain lake	Wood	Mean CD	0.31, 0.27	0.03	0.01	0.91	0.01	t: 1.2, p = 0.1
	Floodplain lake	Leaf litter	Mean CD	0.27, 0.24	0.07	0.01	0.87	0.003	t: 3.1, p = 0.01
	Floodplain lake	Rocks	Mean CD	0.53, 0.06	0.19	0.01	0.9	0.01	t: 2.5, p = 0.4
	Floodplain lake	Sand bank	Mean CD	0.63, 0.001*	0.4	0.02	0.97	0.003	t: 1.3, p = 0.18
	Channel	Wood	Mean CD	0.13, 0.57	0.29	0.02	0.92	0.001	t: 5.5, p = 0.01
	Channel	Leaf litter	Mean CD	0.42, 0.12	0.18	0.02	0.97	0.01	t: 1.9, p = 0.05
	Channel	Rocks	Mean CD	0.28, 0.24	0.45	0.02	0.99	0.003	t: 7.5, p = 0.01
	Channel	Sand bank	Mean CD	0.34, 0.23	0.12	0.01	0.91	0.004	t: 1.9, p = 0.05
Neches	Floodplain lake	Wood	Mean CD	0.14, 0.61	0.02	-0.01	0.92	0.002	t: 2.2, p = 0.03
	Floodplain lake	Leaf litter	Mean CD	0.30, 0.23	0.09	0.01	0.97	0.002	t: 3.3, p = 0.02
	Channel	Rocks	Mean CD	0.78, 0.01*	0.61	-0.04	0.94	0.002	t: 3.2, p = 0.02
	Channel	Wood	Mean CD	0.21, 0.32	0.05	-0.01	0.89	0.003	t: 3.8, p = 0.02
	Channel	Sand bank	Mean CD	0.38, 0.07	0.15	-0.02	0.88	0.004	t: 3.6, p = 0.01
Brazos	Floodplain lake	Wood	Mean CD	0.29, 0.22	0.08	0.02	0.98	-0.01	t: 3.8, p = 0.01
	Floodplain lake	Leaf litter	Mean CD	0.18, 0.41	0.03	0.01	0.89	0.003	t: 2.7, p = 0.02
	Channel	Rocks	Mean CD	0.03, 0.91	0.001	0.002	0.96	-0.01	t: 3.9, p = 0.01
	Channel	Wood	Mean CD	0.07, 0.72	0.01	-0.01	0.95	-0.001	t: 5.4, p = 0.1
	Channel	Sand bank	Mean CD	0.26, 0.23	0.07	-0.02	0.89	0.003	t: 4.3, p = 0.01
Tambopata	Floodplain lake	Wood	Mean CD	0.09, 0.74	0.01	-0.01	0.97	-0.03	t: 3.5, p = 0.1
	Floodplain lake	Leaf litter	Mean CD	0.37, 0.18	0.01	-0.01	0.98	-0.01	t: 2.8, p = 0.08

APPENDIX B

Appendix B. Main diet categories of the different cichlid and centrarchid species. Item values are the feeding index (IA) which combines frequency of occurrence and volume of each item.

No ind. Examine	Species	Bryozoa	Diatoms	Algae	Detritus	Vegetal material	Sand	Mollusca	Microfauna	Microcrustacea	Crustacea	Odonata	Coleoptera	Diptera	Ephemeroptera	Hymenoptera	Trichoptera	Fishes	Fish scales	Miscellaneous ad	Standard length ranges (mm)
Cinaruco River																					
21	*A. vultuosa*	0.5			0.4	5.2			2.9	0.1	26.7	3.9	2.6	2	2.1			43.7	5	2.05	73 -95
21	*A. diadema*	0.02	0.02	0.06	3.38	0.8			1	3.1	0.5	3.5	0.1	20	10.3		5.1	13.4	0.4	0.02	81.7 -133
109	*A. hoignei*	0.02	0.24	0.85	4.76	6.3			0.7		9.9	48	0.1	0.1	0.01	3.3	3.17		12.1		19.3 -38.3
125	*Apistogramma sp.*	2.3	0.14	0.27	6.86	1.1			29.7	13.6		15.6		13.2	0.6		10.1			<0.005	15.1 -20
102	*B. wavrini*	0.02	0.01	0.03	0.74	0.3	0.2		2.8	3.04		0.01		86.1	0.1	0.02	0.02	9.5	0.1	0.01	60 -228
128	*B. dicentrarchus*	1.61	0.23		9.23	1.8	0.3		3.4	30.5		0.2		31.9	10.2		10	0.7			23.3 -386
125	*G.abalios*	0.36	0.21	0.41	5.37	4.4	4.8		21.6	0.7		10.3	2.5	12.6	22.3	0.1	14.7	0.4	15.5	0.06	51.3 -271
137	*G. dicrozoster*	0.04	0.01	0.55	2.77	5	2		6	11.4		10.1	0.5	11.2	15.4		13			4.12	90 -205
172	*S. daemon*	0.03	0.37	0.04	2.34	2	4		13.5	1.9		10.7		15.1	11.5	0.2	23		13.1	0.63	115 -275
13	*S. mapiritensis*	0.99	0.1		1.77	1.1	2.5		0	2.1				0.4	1.5	0.4	88.5	0.02	2.7		95 -185
71	*Heros* sp.	4.1	0.6	0.4	13.7	5.2			10.5	4.4	0.1	1.2	8.3	21.3	12.9	0.1	10.7	11.2	15.2	0.52	74 -243
41	*H. psittacus*				4.3				6.2	0.2		13.9	2.8	13.7	22.9	0.2	13.1	15.5	2.2	1.87	68.7 -240
115	*H. coryphaenoides*	0.4	0.2	0.04	1.9	3.8			0.2	0.1	0.5	18.7	0.9	1.3	8.8	0.7	8.23	11.1	34.9	7.78	60 -205
65	*M. insignis*	2.4	0.3	0.3	7.9	7.2			10.3	0.2		14.7	5.1	10.7	5.1	10.3	10.3	3	20.5	0.95	50.5 -133
133	*C. aff. wallacii*	0.2		0.05	3.8	1.2			0.1	1	9	2.4		5	45.9	0.1	7.3	19.1	3.8		29.1 -64
300	*C. lugubris*					0.4			0.3		10.7	2.8		0.1	0.4	0.2		76.1	2.7	0.19	100 -258
114	*C. intermedia*										0.8	2.1						97.4			164 -365
154	*C. orinocensis*										2.2							96.5		1.37	164 -420
254	*C. temensis*										0.2	1.8						98.2			158 -529

Appendix B. Continued

No ind. Examined	Species	Bryozoa	Diatoms	Algae	Detritus	Vegetal material	Sand	Mollusca	Microfauna	Microcrustacea	Crustacea	Odonata	Coleoptera	Diptera	Ephemeroptera	Hymenoptera	Trichoptera	Fishes	Fish scales	Miscellaneous aquatic insects	Standard length ranges (mm)
Tambopata Floodplain lake																					
15	*A. tetramerus*	0.1		0.3	6.8	7.7			10.2	10.1	8.3	10.7	10.5	10.1	3.1	1.8	6.8	4.9	5.3	8.3	84.3 -126
56	*A. luenligi*		0.2	0.9	4	0.4			55.3	10.1			10.5	18.5			10.2				18 -26.2
35	*A. urteagi*	2.1		0.8	2.7				11.3	32.4		11.9		30			5.8				16.5 -38.5
65	*C. amazonarum*	0.6		0.1	4.7	1.7		3.5	0.2	0.02		5.2	0.2	22.9	10.8	3.2	15.2	12.4	10.3	5.1	45 -111.9
72	*S.jurupari*			0.1	6	3.4			13.2	15.1		12.3	5.1	28.9	10.5		0.7			0.2	88.8 -156
25	*M. festivus*	6.5	0.5	2.2	8.1	4.5			11.3	5		2.5	4.9	11.8	15.6	1.1	19.6	2.1		1.6	31.4 -84.6
78	*C. semicincta*			0.8	0.5	4.3			2.5	29.5	0.5	1.3	0.02	2.8	16.6	0.1	14.4	22.6	3.3	0.7	36.2 -156
Neches River																					
33	*L. microlophus*			9.7				71.4					5.5		4.3	0.7	2.5				41 -239.7
35	*L. humilis*				4.6			3.4	2.2	2.3		4.1	4.3	12.2	31.2		20.3		1.2		28.5 -68.3
10	*L. miniatus*			5.9	2.1	0.5	2.7			0.03	13.4	53.4		3.7	0.3	0.9	16.3		0.2	0.3	55 -99.8
67	*L. megalotis*	2.2		0.2	2.7	2.1	0.2	5.6	1.1	12.6	6	3.2	1	13	15.3	2.1	8.3	7.1	11.4	2.4	41 -129.5
223	*L. macrochirus*	1.9	0.2	2.2	2	4.8	1.2	0.6	0.3	11	5.1	8	2.4	17.9	10.8	6.3	10.9	5.6	3	3.5	42 -128.1
75	*L. cyanellus*			0.02	3.9				4.7	40.3	6.4	4.8	2.8	11.7	0.9	5.7	6.3	8.3	5.9		34 -90.3
83	*L. gulosus*				0.9	1.2		4.4		3.6	8.6	12.3		0.6	2.7	3.4	1.3	58.2		3	35 -91
126	*P. annularis*								<0.005	0.02	16.6			1.5	1.9	0.7		75.7			40.8 -260
34	*P. nigromaculatus*							0.6			12.5	4.3	3.4	10.6	6.2	3.3	1.9	49.2		8	95 -202
86	*M. salmoides*					1.8				3.5	30.5	0.5		0.2	<0.005	1.1		66			49 -375
107	*M.punctulatus*					1				0.01	24	1.1	0.1	0.4	2.4	1.2		66.7	2.5	0.2	35 -460

Appendix B. Continued

No ind. Examined	Species	Bryozoa	Diatoms	Algae	Detritus	Vegetal material	Sand	Mollusca	Microfauna	Microcrustacea	Crustacea	Odonata	Coleoptera	Diptera	Ephemeroptera	Hymenoptera	Trichoptera	Fishes	Fish scales	Miscellaneous aquatic insects	Standard length ranges (mm)
Brazos River																					
20	*L. microlophus*							84.3		5		3.8		3.5		1.9		1.9			41 -110.8
56	*L. humilis*				0.62					9.79	4.4	5.5	0.3	13.3	24.9	3.4	23.1			1.08	30 -80.6
14	*L. miniatus*	0.3		4.4	6.1	1.5	0.3	0.2	3.9	3.4		5.2	1.2	59.5		2.6	5.4		0.6	3.2	40 -77.8
164	*L. megalotis*	0.1	0.03	0.5	1.2	0.1	3.8	0.5		29.4		1.9	1.4	27.9		0.9	12.6	8.4	3.1	4.2	40.2 -93.1
119	*L. macrochirus*	0.6		2.4	7.6	1.5	0.3	1.9	0.1	0.8	0.6		0.4	41.7	22.6	1.5	10.6	2.4	1.1	1.4	49.3 -94.5
98	*L. cyanellus*	1.9		0.1	2	0	0.04	12.3	6	2.2	0.1	16.1	16.6	13	0.3	3.3	13.1	11.2		2	30 -113
68	*L. gulosus*				0.4	4.4	0.04	1.2		0.1	57.9	0.8		1.1	0.1	2.7		30.3		1	38 -126.9
188	*P. annularis*			0.03	0.04	2				1.8	19.1	19.5		1.3	0.1	4.3		51.1		0.6	40 -174
74	*M. salmoides*									3.1	19.2	0.5			0.1	2.6		73.5		1.1	50 -315
85	*M. punctulatus*			0.01		0.03			<0.005		35.5	1.6	0.1	0.02	2.5	2.9		57.4			40 -230